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Source: Ornithological Monographs No. 69

Published By: American Ornithological Society

URL: https://doi.org/10.1525/om.2010.69.1.1

Ornithological Monographs
Volume (2010), No. 69, 1–30

Printed in USA.

ON THE ORIGIN OF SPECIES THROUGH HETEROPATRIC DIFFERENTIATION: A REVIEW AND A MODEL OF SPECIATION IN MIGRATORY ANIMALS

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Abstract.—Differentiation and speciation without extended isolation appear to be common among migratory animals. Historical oversight of this is probably due to temporal distortion in distribution maps and a tendency to consider that lineages had different historical traits, such as being sedentary or much less mobile. Mobility among cyclic migrants makes population isolation difficult, and diminished levels of intraspecific differentiation occur in avian migrants (I term this "Montgomery's rule"). Nevertheless, many lineages have differentiated despite increased mobility and a high propensity for gene flow, conditions that speciation theory has not addressed adequately. Populations of seasonal migrants usually occur in allopatry and sympatry during a migratory cycle, and this distributional pattern (heteropatry) is the focus of a model empirically developed to explain differentiation in migratory lineages. Divergence arises through disruptive selection from resource competition and heterogeneously distributed cyclic resources. Heteropatric speciation is a type of ecological speciation in which reproductive isolation increases between populations as a byproduct of adaptation to different environments that enhances breeding allopatry and allochrony despite degrees of sympatry that occur during the nonbreeding period in migration cycles. Mating or pair bonding in nonbreeding areas is rare. Patterns such as leapfrog migration and limited morphological divergence suggest that differentiation is driven by these ecological factors rather than by sexual selection or nontemporal changes in the resource base itself, although the additional presence of either of the latter would have additive divergent effects. Migratory lineages provide a largely neglected series of natural experiments in speciation in which to test predictions stemming from this model and others focusing on ecological speciation.

Key words: adaptation, allopatric speciation, cyclic migration, ecological speciation, leapfrog migration, migratory lineages, sympatric speciation.

Sobre el Origen de las Especies Mediante Diferenciación Heteropátrica: una Revisión y un Modelo de Especiación en Animales Migratorios

Resumen.—La diferenciación y la especiación en ausencia de aislamiento extendido parece ser común entre los animales migratorios. Es probable que el haber pasado por alto este patrón históricamente se deba a la distorsión temporal de los mapas de distribución y a una tendencia a considerar que los linajes presentaban rasgos distintos anteriormente, como ser sedentarios o mucho menos móviles. La movilidad de los migrantes cíclicos hace que el aislamiento de las poblaciones sea difícil y existen niveles reducidos de diferenciación intraspecífica en las aves migrantes (denomino a esto la "regla de Montgomery"). Sin embargo, muchos linajes se han diferenciado a pesar de su alta movilidad y de ser propensos al flujo genético, condiciones que la teoría sobre la especiación no ha abordado adecuadamente. Las poblaciones de migrantes estacionales usualmente se encuentran en alopatría y en simpatría durante un ciclo migratorio y este patrón de distribución (heteropatría) es el foco de un modelo desarrollado empíricamente

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Ornithological Monographs, Number 69, pages 1–30. ISBN: 978-0-943610-88-7. DOI: 10.1525/om.2010.69.1.1.

para explicar la diferenciación en los linajes migratorios. La divergencia surge mediante selección disruptiva como consecuencia de la competencia por recursos y de la distribución heterogénea de recursos cíclicos. La especiación heteropátrica es un tipo de especiación ecológica en la que el aislamiento reproductivo entre poblaciones aumenta como un subproducto de la adaptación a diferentes ambientes que permite la reproducción alopátrica y alocrónica a pesar de los grados de simpatría que se presentan durante el período no reproductivo en los ciclos migratorios. El apareamiento y el establecimiento de vínculos de pareja son raros en las áreas no reproductivas. Patrones como la migración tipo salto de rana y la variación morfológica limitada sugieren que la diferenciación es impulsada por esos factores ecológicos y no por selección sexual o por cambios no temporales en la base de recursos misma, aunque la presencia adicional de cualquiera de los últimos tendría efectos divergentes aditivos. Los linajes migratorios brindan una serie de experimentos naturales sobre especiación hasta ahora ignorados en buena parte y que permiten poner a prueba las predicciones derivadas de este modelo y de otros enfocados en la especiación ecológica.

INTRODUCTION

SPECIATION THEORY HAS long been approached from the perspective of how diverging populations are distributed. Observations of differentiation in allopatric populations led to the elucidation and widespread acceptance of the geographic, or allopatric, model of speciation (Mayr 1942, 1947, 1999). It is easy to understand how geographically separated populations have levels of gene flow that are low enough to enable them to diverge. Two other distributional categories that have dominated speciation theory are sympatry and parapatry. However, the allopatric model has been thought to be the predominant mode of speciation, and plausible alternatives have been relatively few (Feder 1998, Futuyma 1998, Albertson et al. 1999, Simon et al. 2000, Coyne and Orr 2004, Price 2008). Besides the long-perceived absence of good examples of nonallopatric speciation in natural populations, relevant theory has until recently been insufficiently developed to accept alternative routes to speciation. Rapid development of speciation theory in the past decade has made alternative modes of speciation more popular, but good examples of alternatives to allopatric speciation remain few (Coyne and Orr 2004, Price 2008, Templeton 2008).

Using birds as examples, I suggest that differentiation and speciation without multigenerational spatial isolation, the linchpin of the allopatric speciation model, is a common phenomenon among seasonally migratory animals. Widespread oversight of this phenomenon is probably due, in part, to theoretical models and approaches that largely exclude seasonal migrants, perhaps because their increased movements and distributional status are difficult to accommodate. However, even among those who study migratory organisms, intellectual development of the interactions between seasonal migration and differentiation has been stunted by (1) a failure to recognize temporal distortions inherent in the mapping of breeding distributions and (2) a nearly ubiquitous tendency to consider that lineages had historical traits that they no longer possess, such as sedentariness or greatly diminished dispersal abilities (both are considered in detail below). Together these factors seem to have resulted in an oversight of what is likely to be a common form of differentiation and speciation that has little to do with the type of allopatry so important to the allopatric speciation model.

My initial hypothesis, then, is that the allopatric speciation model is inadequate to explain a lot of the differentiation that occurs in migratory lineages and, consequently, that a different model is required. I use "migration" to refer to cyclic, recurring organismal movement, rather than as a term commonly used in genetics for effective gene flow. In birds migration cycles tend to occur with an annual periodicity, as a go-and-return phenomenon, with reproduction occurring at one end of the spatial cycle. The relationship between migratory movements and evolutionary divergence demands increased study if only because these cyclic movements are so common. For example, migratory birds represent more than 50% of the avifauna of the United States (338 of 650 species; Rappole 1995), and they probably total billions of individuals (see Moreau 1972).

This monograph fully develops the rationale and details behind my earlier suggestion (Winker 2000) that a new theoretical framework is needed to understand speciation in migratory lineages. As I review the subject of differentiation in migratory lineages, I will outline the difficulties of applying allopatric speciation models to these animals. I will then describe a new alternative model (heteropatric speciation), list potential criticisms of this model, and provide some suggestions for its evaluation. Finally, I will give a forward-looking glimpse into how research on this topic might continue.

FLYING THE AERIAL SEAS, OR THE CONTINENTAL PELAGISTS

Mayr (1963:583, 1993:138) recognized problems with the allopatric model of speciation in pelagic situations, where it is difficult to envision the barriers so important to this model. Seasonally migratory birds are both terrestrial and oceanic equivalents to these problematic aquatic organisms. The semiannual transcontinental and transoceanic movements of migratory birds endow them with the same unlikelihood of being placed into the box of multigenerational spatial isolation required by the allopatric model of speciation.

Migration has arisen independently among many lineages (Baker 1978, Alerstam et al. 2003). But it is not so easily gained and lost within a lineage that we can consider that every migratory lineage or group in which differentiation has occurred has involved a cessation of migration or a period of spatial isolation between lineages long enough in evolutionary time to allow differentiation to result in speciation before migratory behaviors were once again resumed. This seems an obviously inappropriate contortion of history, clearly violating the principles of parsimony and likelihood. Yet to make differentiation in migratory avian lineages fit the allopatric model, scenarios for speciation in these groups have routinely imposed isolation (e.g., Dilger 1956, Mengel 1964, Cox 1985), which implicitly invokes mechanisms such as lower historical levels of migration and greater levels of natal philopatry than are presently exhibited. Mentally changing lineage attributes to fit a model must be avoided. More recent studies (e.g., Lovette and Bermingham 1999, Weir and Schluter 2004) continue to focus on isolation through fragmentation of breeding habitat (ignoring nonbreeding distributions), but in not asking or answering the question of what scale of habitat fragmentation is necessary to achieve true allopatry between lineages that often exhibit movements at continental scales, they prolong this historical trend of ignoring the presence and scale of migratory movements. To be fair, both Lovette and Bermingham (1999) and Weir and Schluter (2004) moved beyond a strictly allopatric process and suggested that speciation in the migrants they studied occurred with gene flow, but only after prolonged periods of isolation during glacial maxima. I question this assumption of isolation, both because of the relative scale and importance of extant movements (and the likelihood that ancestors had similar traits) and because we need to consider spatiotemporal overlaps during the full annual cycle.

Long-distance seasonal migration, in particular, represents a complex behavior with multiple associated characteristics, such as seasonal fat deposition and genetically controlled timing and orientation mechanisms (e.g., Berthold 1988, 1993, 2003). The most parsimonious reconstruction of evolutionary history may not always be correct, but it is preferable to consider that migratory lineages and groups tend to retain complex characters once they have been attained. Mayr (1942:55) recognized this, stating that "The presence or absence of migratory movements in birds belongs as much to the genetic characteristics of a race or species as does size or color patterns." Later authors overlooking this important consideration have prolonged an inappropriate adherence to the allopatric model of speciation to explain differentiation in migratory lineages.

Among migratory organisms the relationship between migration and the process of differentiation is circumscribed by two important facts: escape into multigenerational allopatry is difficult, and seasonal sympatry among potentially differentiating lineages is common.

MOVING PAST "MONTGOMERY'S RULE"

Montgomery (1896:461) recognized that "the amount of geographical variation in species with more or less extensive breeding areas, stands in inverse ratio to the extent of its periodic migrations." Rensch (1933) came to a similar conclusion, and Mayr (1963:582) stated that sedentary species averaged twice as many subspecies as migratory species. Vagility, vagrancy, and dispersal abilities are notoriously high among migratory birds (Grinnell 1922, Wetmore 1926, Böhning-Gaese et al. 1998, Belliure et al. 2000), and it is indisputable that these increases in movement and the corresponding increases in the propensity for gene flow can have a dampening effect on the process of differentiation. But the simple conclusion that migration counters differentiation explains only part of the relationship between these two phenomena. There remains a considerable degree of differentiation occurring among migratory lineages.

Differentiation within migratory lineages occurs at multiple organizational levels (populations through species and beyond), and this is easily recognized through examination of subspecies. I consider the use of subspecies here as a heuristic tool lending insight into the partitioning of variation within species. Beyond providing such insight, the utility of this traditional approach is limited, and this is discussed further below. Subspecies have been important in elucidating the processes of evolution and speciation (Mayr 1963, Zink and Remsen 1986, Winker 2010), and subspecific differentiation is correlated with demographic parameters, such as dispersal, that are important to gene flow and the process of divergence (e.g., Belliure et al. 2000). Further, Martin and Tewksbury (2008) showed that the maximum number of subspecies in a species within a genus covaries positively with the number of species in that genus; this likely reflects that a lineage's propensity to differentiate is an attribute that it holds for a substantial period of evolutionary time—well through the speciation process and observable at the subspecies level. Polytypy, or formally recognized subspecific differentiation, occurs in approximately half of all migratory bird species within the world's three largest and best-documented migration systems (Table 1).

Table 1. Numbers of polytypic migratory avian species by family (over total possible in system) within each of the world's three largest and best-documented migration systems. Species are assessed independently within each migration system. Thus, a species can be represented more than once across migration systems, but polytypy is counted only when it occurs within a system (polytypy across systems is not counted, nor is it counted if differentiation occurs outside the "cruising range" [Mayr 1963] of the migratory form). Many of the world's migratory species are not included (for many occur outside these systems); lists of migrants are based on appendices in Rappole (1995) and taxonomic assessments on Peters et al. (1934–1987).

Taxon	Nearctic–Neotropic	Palearctic–African	Palearctic–Asian
Podicipediformes			
Podicipedidae	2/3	0/1	0/1
Pelecaniformes			
Pelecanidae	1/2		1/2
Phalacrocoracidae	1/2		1/1
Anhingidae	0/1		
Ciconiiformes			
Ardeidae	7/12	3/8	4/16
Threskiornithidae	0/4	1/3	1/4
Ciconiidae	0/1	0/2	1/6
Cathartidae	1/2		
Anseriformes			
Anatidae	5/20	0/11	3/19
Falconiformes			
Accipitridae	6/11	8/17	9/23
Falconidae	3/4	3/8	4/6
Galliformes			
Phasianidae		1/1	1/1
Gruiformes			
Rallidae	4/7	2/5	6/8
Gruidae	1/2	0/2	0/2
Charadriiformes			
Burhinidae			1/1
Rostratulidae			0/1
Charadriidae	3/8	2/7	4/12

(*continued*)

TABLE 1. Continued.

Taxon	Nearctic–Neotropic	Palearctic–African	Palearctic–Asian
Haematopodidae	1/1	1/1	1/1
Recurvirostridae	0/2	0/2	0/2
Jacanidae			0/1
Scolopacidae	4/30	3/23	5/38
Glareolidae		1/2	0/1
Laridae	7/23	3/11	6/17
Columbiformes			
Columbidae	4/5	1/1	2/2
Cuculiformes			
Cuculidae	2/3	1/2	7/10
Strigiformes			
Strigidae	3/3	1/2	2/3
Caprimulgiformes			
Caprimulgidae	4/5	3/3	
Apodiformes			
Apodidae	3/4	4/4	6/6
Trochilidae	8/13		
Trogoniformes			
Trogonidae	1/1		
Upupiformes			
Upupidae		1/1	1/1
Coraciiformes			
Alcedinidae	1/1		2/2
Meropidae		0/1	2/2
Coraciidae		1/1	1/1
Piciformes			
Picidae	2/3	1/1	1/1
Passeriformes			
Tyrannidae	16/32		
Laniidae	1/1	5/6	2/3
Vireonidae	6/10		
Oriolidae		1/1	5/7
Campephagidae			5/5
Dicruridae			3/4
Alaudidae		2/2	2/2
Hirundinidae	5/8	5/5	4/5
Troglodytidae	3/3		
Regulidae	1/1		
Pycnonotidae			1/1
Sylviidae	1/1	19/29	31/45
Muscicapidae		3/3	15/21
Turdidae	8/10	13/18	22/31
Zosteropidae			1/2
Mimidae	0/2		
Sturnidae			1/6
Motacillidae	1/2	3/6	9/13
Bombycillidae	0/1		
Parulidae	16/50		
Thraupidae	3/6		
Emberizidae	14/17	1/3	3/6
Cardinalidae	2/6		
Fringillidae	2/2		4/4
Ploceidae		0/1	
TOTALS	161/338	93/194	180/346

Although movement rates among long-distance migrants (i.e., populations and species) are high, rates of successful intercontinental colonization across migration systems are not (as evidenced by the relatively few species that have populations within multiple migration systems). This may seem counterintuitive, but it fits well with the rather widely accepted and taxonomically well-supported "southern home" (or "nonbreeding ground") hypothesis for the origins of most migratory lineages (Rappole 1995; though see Gauthreaux 1982). This hypothesis considers that most long-distance migrants fly to breeding grounds at higher latitudes to exploit seasonally abundant resources for reproduction, then return to more or less ancestral places of origin at lower latitudes between reproductive attempts. Their poor ability to colonize new continents outside of their original migration system is thought to reflect a difficulty in establishing new wintering grounds, which probably occurs far less frequently than the colonization of new breeding grounds because it runs counter to deep genetic programming in the direction of migration required for returns to ancestral (i.e., suitable nonbreeding) areas (see Lack 1968; Berthold 1993, 2003; Rappole 1995; Böhning-Gaese et al. 1998; Bensch 1999; Joseph et al. 1999). In short, regardless of whether the southern home hypothesis is a definitive explanation for this phenomenon, there is a greater degree of isolation across, versus within, migration systems.

Nevertheless, many migratory species have successfully made intercontinental colonizations and presently occur in two or more of the world's three major migration systems (Peters et al. 1934–1987, Rappole 1995). The hypothesis that migration counters differentiation (i.e., Montgomery's rule) would predict that for these species differentiation would be more likely to occur across rather than within these systems. Following Rappole (1995) and Peters et al. (1934–1987), it can be seen that of the 102 species that occur in two or more of the world's three largest migration systems (Nearctic–Neotropic, Palearctic–African, and Palearctic–Asian), 40 exhibit no differentiation in the context considered here; most, but not all, are monotypic. (Those that are not monotypic are polytypic outside the framework of the question posed here; e.g., they have subspecies described outside the geographic coverage of these migration systems.) These taxa are not further considered, because they do not allow a test of the hypothesis that, because of the relative isolation of major migration systems, differentiation is more likely to occur across rather than within these systems. Of the remaining 62 species, 53 (85.5%) exhibit differentiation across migration systems, a pattern that affirms the importance of allopatric differentiation. But fully 56 of these 62 species (90.3%) exhibit differentiation within at least one of the migration systems in which they occur, a frequency of differentiation not significantly different from that found between migration systems (*G*-test with Williams's correction; $P > 0.5$). This indicates that migration does not have a tendency to lower the propensity for differentiation in this group of 62 species.

Classic cases in which migration probably counters differentiation occur in few taxa. One example is the Whimbrel (*Numenius phaeopus*), a species that exhibits no recognized differentiation within any of the three migration systems, but which has a subspecies unique to each, or fully recognizable differentiation across systems. Only six species (9.7%) show this pattern of differentiation occurring across but not within migration systems. Nine species (14.5%) exhibit the opposite condition, that of differentiation within rather than across systems, whereas the majority (47, or 75.8%) exhibit differentiation both within and across migration systems. Thus, among these taxa, there is no greater propensity to differentiate in the comparative isolation that occurs across migration systems than in the much greater population-mixing conditions that occur within systems. Migratory taxa with a propensity to differentiate appear to do so regardless of migration or isolation.

MIGRANT DIFFERENTIATION

Evidence of historical and ongoing differentiation is common among migratory lineages at levels from populations through species and even genera. There are many obvious cases in which what began as subspecific differentiation within a migratory lineage has progressed to full speciation (see Table 1). Some of these are not yet universally recognized by taxonomists, but examples include species complexes such as *Pluvialis "dominica"* (Connors et al. 1993, American Ornithologists' Union [AOU] 1998), *Empidonax "traillii"* (Stein 1963, AOU 1998, Johnson and Cicero 2002), *E. "difficilis"* (Johnson and Marten 1988, AOU 1998, Johnson and Cicero 2002), *Vireo*

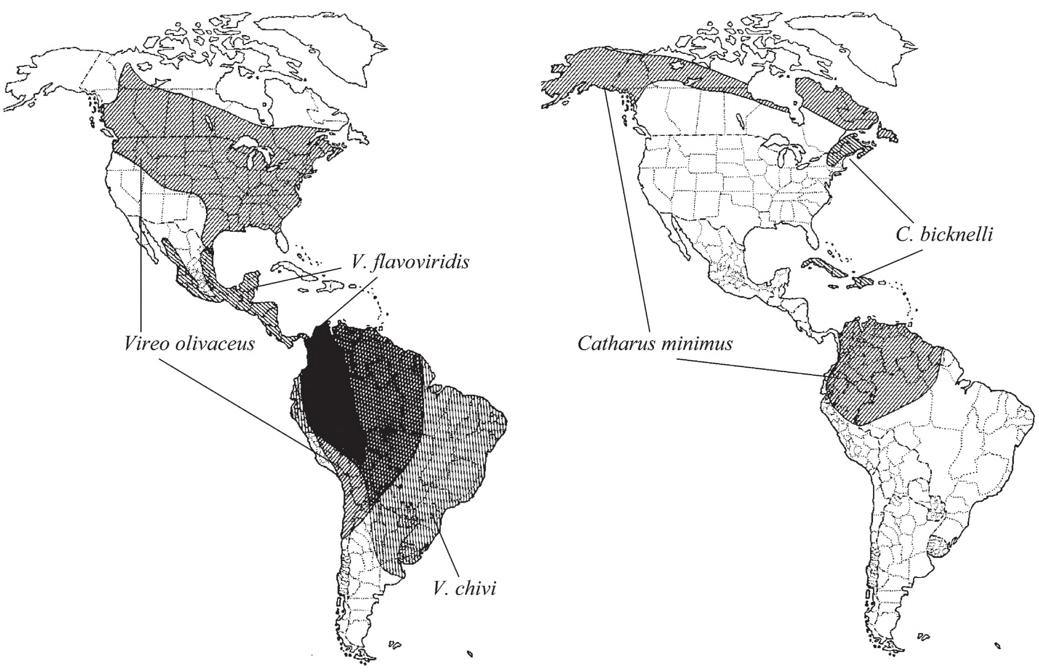

FIG. 1. Breeding and wintering ranges of the *Vireo "olivaceus"* and *Catharus "minimus"* species complexes, exhibiting divergence in migratory lineages and leapfrog migration.

"olivaceus" (Johnson and Zink 1985, AOU 1998; Fig. 1A), *Vireo "solitarius"* (Johnson 1995, AOU 1998), *Catharus "minimus"* (Ouellet 1993, AOU 1998; Fig. 1B), *Dendroica "petechia"* (Klein and Brown 1994), *Phylloscopus "collybita"* (Helbig et al. 1996), *Passerella "iliaca"* (Zink 1994), and *Loxia "curvirostra"* (Groth 1993, Benkman et al. 2009). The taxonomic labeling of the units involved in the process of differentiation is imperfect, but these and many other examples represent migratory lineages within which reproductive isolation has been achieved between sublineages; speciation has occurred in the presence of migration.

Among some of these taxa—for example, *Dendroica "petechia," Vireo "solitarius," Piranga* (Burns 1998), and Baltimore Orioles (*Icterus galbula*) and Black-backed Orioles (*I. abeillei*) (Kondo et al. 2008)—the mapping of migration onto the phylogenetic trees shows that some of the differentiation or speciation is correlated with a subgroup of the ancestral lineage dropping out of migration to establish resident, nonmigratory (or less migratory) breeding populations, usually in tropical or subtropical regions (Klein and Brown 1994, Johnson 1995, Burns 1998, Cicero and Johnson 1998, Kondo et al. 2008). Several sedentary Caribbean species in the genus *Vireo* may also be found to be members of the *V. "olivaceus"* species group (Fig. 1A), which would likely represent a similar pattern. Another pattern is that of the origin and subsequent differentiation of migratory populations while sedentary, presumably ancestral populations remain extant (Peters et al. 1934–1987, Salomonsen 1955). Both of these patterns reflect differentiation in the face of migratory movements and usually some degree of sympatry as well. Both also seem difficult to accommodate under the allopatric model. For example, many of these derived nonmigratory populations seem to drop out of migration to subsequently differentiate in what might be considered high-traffic areas because of the cyclic migrations of conspecific populations.

Range shifts unquestionably occur among these animals, and current breeding distributions, in particular, must be considered carefully because of factors such as postglacial expansions. However, the gross patterns that commonly occur among these lineages, such as nonbreeding sympatry, range patterns (e.g., leapfrog migration), and the overall scope of movements, seem to preclude ready application of allopatry as the condition enabling differentiation.

Going deeper, below the twig level of avian dendrograms, the mapping of long-distance migration onto phylogenies shows that the origin of this behavior often preceded substantial levels of differentiation in genera such as *Calidris* (Borowik and McLennan 1999), *Phalaropus* (Dittmann and Zink 1991), *Tringa* (Pereira and Baker 2005), *Sphyrapicus* (Cicero and Johnson 1995), *Vireo* (Cicero and Johnson 1998), *Dendroica* (Bermingham et al. 1992, Lovette and Bermingham 1999), *Piranga* (Burns 1998), and *Phylloscopus* (Richman 1996, Price et al. 2000).

Migration alone does not account for all of the diversity in these groups, but these observations caused me to suggest that the origin of migration may, in some cases, represent a key innovation that enabled a lineage to encounter, exploit, and ultimately differentiate to fill new niches in more seasonal environments that were temporally or geographically unavailable to their ancestors (Winker 2000).

Leapfrog migration.—Leapfrog migration occurs when populations, subspecies, or even sibling species from higher latitudes migrate to wintering grounds at lower latitudes than other populations (or subspecies or species). The ranges of the latter are passed through twice each cycle during the migrations of the former. It is such a common phenomenon that Baker (1978:696) felt that, at the population level, many if not most landbird species exhibited this characteristic. It is usually recognized through movements of populations that are morphologically recognizable as distinct subspecies, but it also occurs among full species (Salomonsen 1955, Lundberg and Alerstam 1986, Boland 1990, Kondo et al. 2008; Fig. 1).

It is difficult to conceive of the phenomenon of leapfrog migration as a product of allopatric differentiation. Yet it is common and recognizable across a spectrum of levels ranging from the slightly differentiated to species clades (Peters et al. 1934–1987, Salomonsen 1955). The commonness of the phenomenon plainly demonstrates that differentiation can proceed directly in the path of high rates of movement. But how can this differentiation accrue and persist?

SPATIAL AND TEMPORAL DISTRIBUTIONS OF MIGRANTS

Traditional maps and descriptions of the breeding ranges of migratory birds are artificially static. They tend to compress time into a nondimensional attribute, failing to portray important temporal information and imparting a bias that is difficult to overcome. What is not portrayed is that populations at higher latitudes frequently occur in sympatry with populations at lower latitudes, often when the latter are reproducing.

In other words, our summaries of avian distributions overlook the simple fact that among migrants the breeding season begins and then progresses gradually, increasing in latitude (Baker 1938) and elevation, so that the last individuals to breed are commonly found in sympatry with populations from which they are diverging or have diverged. This often occurs during or very close to the reproductive periods of the latter. For example, in southern Veracruz, Mexico, migrant Red-eyed Vireos (*V. olivaceus*) are present through more than the first month of the breeding season of locally reproducing Yellow-green Vireos (*V. flavoviridis*; breeding-condition dates: 10 April–25 May; M. Ramos pers. comm.; specimens in Bell Museum of Natural History, University of Minnesota; Fig. 1A). Similarly, migrant Gray-cheeked Thrushes (*Catharus minimus*) occur in the breeding range of Bicknell's Thrushes (*C. bicknelli*), and even as far south as Kansas, well into the egg-laying period of the latter (egg dates: 3 June–14 July; Wallace 1939, Phillips 1991, Marshall 2001; Fig. 1B).

The fact that the migrants that travel farther breed elsewhere and at another time is an important, but at this point secondary, consideration. Most important among differentiating and differentiated lineages is that these populations are not interbreeding when they are in sympatry, or, if they are, it seems likely (given ongoing differentiation) that such crosses are either very rare or less fit (e.g., Helbig 1991). Considering that individuals that occur together have the opportunity to reproduce, the fact that they do not is an important observation. By artificially simplifying tremendous variation in spatial and temporal distributions, our maps and descriptions of breeding distributions have caused us to overlook this profoundly important degree of sympatry commonly found among migrants.

There is also considerable variance in the spatiotemporal distributions of avian migrants (e.g., compared with those of resident taxa). Subspecies- and species-level averages in the timing of migration (e.g., Ramos 1988, Winker and Rappole 1992) and the individual capacity for philopatry (return to origin) can be remarkably precise. But the tails of the distributions in time and space are notoriously long; indeed, migratory movement often seems to be quite sloppy (Grinnell 1922). Thus, in lineages in which differentiation has occurred, it is not likely to have arisen because a single genetic change caused a precise switch in the timing and place of reproduction and a consequent cessation of gene flow between groups.

Propensity for gene flow.—The possibility of gene flow among migrant populations, particularly early in the process of differentiation, must be relatively high, whether through flexibilities in philopatry, pair bonding, or gamete mobility. For example, breeding populations may experience gene flow if pair bonding occurs during the nonbreeding season when different breeding populations occur in sympatry (a specialized case of flexibility in philopatry). And even among birds, in which nearly all reproductive activities must occur in a nonmigratory state (unlike in mammals, for example), fertilization could apparently occur rather easily between individuals from different populations through gamete mobility. Quay (1986, 1989) demonstrated that males of many species exhibit sperm release while still in migration, well before arriving on their breeding grounds, and that females of at least one species have copulated during migration. Passage of migrants through conspecific breeding populations (or other putatively nonbreeding sympatry between breeding populations) could thus provide geographic mobility in gamete availability and potential fertilization (e.g., through sperm storage). Either of these examples of individuals or gametes moving between breeding populations should increase the likelihood of population crossing and ultimately decrease or stop divergence.

There is a natural experiment in the natural history of birds that tests this hypothesis. Migratory waterfowl (Anatidae) commonly form pair bonds on the nonbreeding grounds or wintering range (Palmer 1976), rather than on the breeding grounds as most migratory birds do. The consequences of this are as expected: with frequent interbreeding of individuals from different breeding populations, migratory species of the Anatidae show a significantly lower propensity for subspecific differentiation than the rest of the class Aves (G-test with Williams's correction, $G_{\text{adj}} = 11.7$, $P < 0.001$; Table 1). This serves as a reminder that such interbreeding between populations does not generally occur among most avian migrants, despite frequent sympatry.

Together, overlap in both spatiotemporal distributions and reproductively active periods provide migrant populations with the increased propensity for gene flow that probably explains Montgomery's rule. I see no evidence, however, that migratory lineages in which differentiation occurs are any less prone to these conditions.

HETEROPATRIC SPECIATION

Because so many migratory populations, subspecies, and species exist in both allopatry and sympatry at different times of the annual cycle, their spatial distributions require a different categorization, which I term "heteropatry." I define "heteropatric" as the distribution of populations or forms that occur together (sympatric) and apart (allopatric) during a migration cycle, and "heteropatric speciation" as divergence between populations that exhibit this distributional condition. The fact that differentiation continues under such conditions suggests that allopatric speciation is not an adequate model for differentiation in these organisms. As can be seen from the previous sections, the contortions required to apply the tenet of multigenerational spatial isolation to all of the cases in which differentiation has occurred in migratory lineages make this model untenable. However, because there is clearly a component of allopatry between diverging populations, models for speciation in sympatry also seem unsuitable.

Nevertheless, because sympatric speciation theory considers differentiation in the context of a high propensity for gene flow, this body of theory is probably more applicable to migrants than the allopatric model (e.g., Maynard Smith 1966, Dieckmann and Doebeli 1999, Higashi et al. 1999, Kondrashov and Kondrashov 1999, Doebeli and Dieckmann 2000, Bolnick and Fitzpatrick 2007). Conceptually, models of sympatric speciation represent the other end of a continuum from allopatric models. But this other end is as unsatisfactory in explaining differentiation among migratory animals as the allopatric model. There are considerable degrees of both sympatry and allopatry involved among these migrant lineages (occurring at different times of the movement cycle), and each must be considered in developing a model to explain differentiation in these organisms. Diverging migratory populations are often effectively cyclic occupants of this entire distributional spectrum.

Although a considerable degree of genetic sorting seems to occur in sympatry among differentiating

TABLE 2. Contrasting three models of sympatric speciation and a general model of allopatric speciation with the proposed model of heteropatric speciation.

	KK[a]	DD[b]	HTY[c]	Allopatric[d]	Heteropatric
Nature of model	Deterministic	Stochastic	Stochastic(?) and deterministic	Stochastic	Stochastic
Resources	Discontinuous	Continuous	Immaterial(?)	Continuous or discontinuous	Discontinuous
Selection regime	Disruptive	Disruptive	Runaway sexual	Neutral or disruptive	Disruptive
Mating	Assortative	Assortative	Assortative	Random or assortative	Assortative
Disequilibrium	Small amount assumed	Arises stochastically	Random, nonnegative	Arises stochastically	Arises stochastically
Environment	Change inferred—required?	Change unnecessary?	Change required	Change unnecessary	Cyclic–seasonal (different elsewhere)
Population size	?	Small	Large is best	Large or small	Large
Number of loci	Higher	Lower	Probably few	Many or few	Probably few
Gene flow	Low	Low	Low	None	Low

[a] Kondrashov and Kondrashov 1999.
[b] Dieckmann and Doebeli 1999.
[c] Higashi et al. 1999.
[d] Including vicariant and peripatric modes (Coyne and Orr 2004).

populations of migratory birds (through and beyond the level of full species), there is a considerable degree of allopatry involved as well. (In fact, it is this breeding-ground allopatry that has maintained the allopatric speciation model as the dominant hypothesis for differentiation among migrants.) In contrasting the characteristics of a heteropatric model of speciation with several sympatric models and a general model of allopatry, it appears that none of the latter two fit what seems to occur in migratory lineages (Table 2). The differences, and the need for a new model, go beyond the simple semantics of distributional labels.

The model.—The heteropatric model proposed here is as follows. Initially, divergence is low. Disruptive selection occurs between populations as a result of fitnesses varying in space; allopatric (or parapatric) resource exploitation during any period in the cyclic movements of diverging populations can cause these fitness differences and the corresponding disruptive selection. A prezygotic isolating mechanism exists through assortative mating and a geographic reproductive setting that differs between populations; the force of selection is transmitted to the isolating mechanism through indirect selection. A genetic basis for increased isolation is likely to be a multilocus mechanism. I have borrowed components of this model from other speciation models to obtain an outline of a new model that fits the biology of differentiating migratory populations. This model has no apparent precedent (see Kirkpatrick and Ravigné 2002, Bolnick and Fitzpatrick 2007).

Kirkpatrick and Ravigné (2002) classified 62 models of speciation into five major elements. Under their scheme, heteropatric speciation would be classified as having conditions I.A (a form of disruptive selection in which fitness varies in space), II.B and C4 (a prezygotic isolating mechanism with assortment traits that include a geographic component; I've added 4 for heteropatry), III.B (selection operates indirectly on the isolating mechanism), IV.B (the genetic basis for increased divergence is multi-allelic), and V.A (divergence is initially low; see Kirkpatrick and Ravigné 2002:S24). Gavrilets (2003, 2004) simply considered all model space between allopatry and sympatry "parapatric," but this label is inappropriate for cyclic migrants. Such simplifications are often required to make the mathematics of theory tractable. But theory is developed to help us understand the speciation process, and it is important to recognize when aspects of that process have been inadvertently omitted from theoretical models. Seasonal migrants exhibit increased levels of movement and heteropatric distributions; distributionally, they occupy all model space from allopatry to sympatry. This vacillating, cyclic aspect of their natural history has yet to be appropriately encompassed in speciation theory.

Schluter (2001) and Via (2001) emphasized the importance of moving away from a distributional focus on modes of speciation to one that is, instead, mechanism oriented. Kirkpatrick and Ravigné (2002:S26) suggested that geography might be considered "simply another form of assortative mating." Butlin et al. (2008) promoted a more sophisticated approach, recognizing variation on spatial and other axes during speciation. These are all useful approaches, but distribution remains a critical component of speciation (e.g., Rice and Hostert 1993; Doebeli and Dieckmann 2003; Gavrilets 2003, 2004; Coyne and Orr 2004; Butlin et al. 2008; Price 2008), and existing theory does not yet adequately encompass heteropatry. Geography can be set aside to focus on the mechanisms of speciation—that is, the accrual of isolating mechanisms through drift, natural selection, and sexual selection. But a full understanding of how those mechanisms operate in natural populations requires reintegration with organismal natural history, in which distribution is naturally important. As Coyne and Orr (2004:85) stated, "biogeography can limit the nature and strength of evolutionary forces potentially causing reproductive isolation." I consider that the distributional uniqueness of migrants (heteropatry) and their propensity to differentiate despite increased movement and associated distributional complexities demand a theoretical framework that explicitly deals with these issues. Present theory does not.

Patterns of divergence can exist among diverse taxa at ecotones (e.g., Rappole et al. 1994, Smith et al. 1997). These cases are often deemed nonallopatric (i.e., parapatric or gradient), but their relationship to heteropatric speciation is very tentative. They belong more in the domain of parapatric models, because cyclic migration and heteropatry are not necessarily involved. However, edge-related processes may stimulate migration through, for example, local temporal variance in resource peaks (Ries et al. 2004). Thus, it is possible that ecotone processes are important at initial stages of heteropatric speciation.

Just as in sympatric speciation theory (Matessi et al. 2001, Bolnick 2006, Bolnick and Fitzpatrick 2007), incomplete divergence may be an evolutionarily stable outcome of this heteropatric divergence process. In other words, just as not all subspecies are "little species" or even incipient species (Simpson 1961, Winker 2010), not all diverging migrant populations are going to complete the process of speciation. This is considered further below.

The model proposed here is closest to the divergence-with-gene-flow family of models (Rice and Hostert 1993), Gavrilets's (2003, 2004) very broadly defined parapatric speciation ("when migration between diverging (sub)populations is neither zero nor maximum"), the "adaptive dynamics" models of evolutionary branching in spatially structured populations of Doebeli and Dieckmann (2003, 2005), and the model of van Doorn et al. (2009) that combines natural and sexual selection in driving ecological speciation. But these models do not yet adequately encompass an increased propensity for divergence with increased movement or heteropatry. Here, I will remain focused on the distributional condition (heteropatry). It is common, heretofore largely overlooked, and, together with divergence occurring with increased movement, the most novel aspect of this model. It provides a new perspective for the study of speciation from multiple approaches.

Factors that promote divergence.—A critical observation is that differentiating migratory birds do not effectively cross while in sympatry, even when local conditions are often clearly suitable for reproduction. This seems explicable only on the basis of the availability of different resource peaks at other places and at other times. Typically, it appears that the reproductive efforts of these diverging populations are focused on resources that occur in different places in space and time, a natural result of the seasonal (cyclic) progression of resource blooms that occur in latitude and elevation, for example. Consequently, it appears that resource competition and the release from this provided by heterogeneously distributed cyclic resource peaks comprise the ecological factors that promote divergence. Among migrant populations these peaks simultaneously promote both allochronic and allopatric conditions of reproduction (spatiotemporal allopatry). For many migrants these resource peaks occur through latitudinal and elevational phenological differences, resulting in varying degrees of both spatial and temporal isolation during reproduction.

Distributions of these resource peaks usually seem to be packed tightly enough together in time that a single population cannot reproduce successfully and move elsewhere to exploit another peak.

Reproductive allochrony is thus a critically important factor in heteropatric differentiation and could alone promote divergence (e.g., Feder 1998, Simon et al. 2000, Coyne and Orr 2004, Friesen et al. 2007). However, allopatry is present, and an increase in this condition will have an additive effect. Increasing degrees of allopatry enhance the propensity for divergence through disruptive selection by (1) bringing to bear the greater differentiating selective pressures inherent in an environment that is more heterogeneous overall, (2) further decreasing gene flow (Rice and Hostert 1993, Doebeli and Dieckmann 2003), and (3) enabling divergence to proceed without being stopped or slowed by competitive exclusion.

These effects of allopatry on divergence may explain the long understood relationship in which differentiating avian migratory lineages often exhibit increasing degrees of allohiemy, or wintering allopatry (Lack 1944, 1968; Salomonsen 1955). This phenomenon is best explained by competitive exclusion (Lack 1968, Gauthreaux 1982) and would be an expected outcome when divergence is driven by selection operating on traits such as timing of reproduction and timing and direction of migration rather than on the morphologies and behaviors of feeding, for example. Allohiemy is not an exclusive prediction of the heteropatric model, but its occurrence helps to infer the selective factors operating to promote divergence in migratory lineages.

Considering both spatial and temporal factors, selection would become increasingly disruptive as traits such as fat deposition (cycle energetics), wing shape, timing and direction of migration, timing of reproduction, and other genetically controlled adaptations developed to exploit these different resource peaks. The more heterogeneous the spatiotemporal distribution of these peaks, the more important these traits become. This is a sort of positive-feedback-loop scenario for an enhanced propensity for differentiation among migrants (see also Rice and Hostert 1993, Doebeli and Dieckmann 2003). For example, if the frequency of migratory behavior in a population is correlated with the degree of migratory activity exhibited (distance traveled), then selection on different aspects of migration may operate on a single polygenic trait or on multiple, highly correlated polygenic traits (Pulido et al. 1996). Selection that coupled an increased frequency of migration with increased distance traveled could accomplish rapid change in a lineage (Berthold 2003).

Additional disruptive selection could occur if the resource bases themselves were different—not just heterogeneously distributed in space and time, but rather different in a more fundamental way (e.g., fruits vs. insects, or flying vs. crawling insects). Thus, different feeding behaviors or morphologies might be favored for exploitation—for example, among Red Crossbills (*L. curvirostra*), which are irruptive migrants that have irregular migratory cycles (Benkman 2003). Or habitat divergences might come into play, as in mangrove occupancy in some subspecies of the Yellow Warbler complex (*D. "petechia"*) and the Prairie Warbler (*D. discolor*). The frequency of allopatry and allohiemy among diverging and recently diverged avian migrant lineages suggests that changes in feeding behaviors or morphologies are not a common or strong factor among diverging migratory birds; in other words, competitive exclusion seems prevalent. However, each influence (time, space, resource base) is considered here to potentially have an additive effect on the propensity for divergence. In addition, selection during the nonbreeding season from any of these dimensions could also influence divergence.

Isolating mechanisms and genetics.—Selection related to cycle-timing, spatial distributions, and resources (and factors not considered here, such as drift or isolation by distance) can produce population structure in migratory organisms. But how does reproductive isolation develop between these populations? Barriers to gene flow are not obvious. Immediate cessation of gene flow is not suggested, and it is not required under this model. Both theory (e.g., Gavrilets 2004) and empirical evidence (e.g., Hey 2006, Niemiller et al. 2008, Price 2008) suggest that speciation can occur with low levels of gene flow.

There are ways in which reproductive isolation might become established between populations during ecological speciation: assortative mating, lowered fitness in immigrants or hybrids, and, following Muller (1942), the accumulation of intrinsic genetic incompatibilities (Hendry et al. 2007, Price 2008:398). Ecological speciation can be effectively initiated within tens of generations (Hendry et al. 2000, 2007; Bearhop et al. 2005), and migratory birds can respond rapidly to changing environmental conditions (e.g., Fiedler 2003). This makes genetic incompatibilities seem a less likely component of heteropatric speciation, except in cases in which the process is protracted, allowing time for such incompatibilities to arise. However, it would be premature to dismiss them, because (1) it is possible that such incompatibilities accumulate as rapidly as the square of the rate of divergence, rather than linearly; and (2) complex epistasis, when incompatibilities involve three or more genes, can further accelerate reproductive isolation (Orr 1995, Johnson 2002). Among long-distance avian migrants many migratory traits are multigenic (Berthold 2003), which suggests that genetic incompatibilities may prove important at later stages of protracted divergence in migratory lineages. Nevertheless, assortative mating and lowered fitness among immigrants or hybrids are the more likely isolating mechanisms between initially diverging lineages under the heteropatric speciation model. The process would be initiated by assortative mating and could theoretically even be completed by that mechanism alone. But, of course, progression in divergence to less reversible isolating mechanisms increases the likelihood of the process going to speciation.

It seems that genetic change at a few loci may be all that is required to attain reproductive isolation between groups of organisms with a high propensity for gene flow (Palumbi 1992, 1994; Dieckmann and Doebeli 1999; Higashi et al. 1999; Doebeli and Dieckmann 2000, 2005). For example, Geritz and Kisdi (2000) showed through modeling that divergence can occur in ecologically identical situations under simple genetic scenarios. Additive genetics on a single locus and the addition of another locus for mate choice (two model conditions) both achieved divergence. Assortative mating is key (Doebeli and Dieckmann 2000, 2005; van Doorn et al. 2009; Table 2); it can be very simply achieved genetically, and selection against heterozygotes does not have to be strong for divergence to occur (Geritz and Kisdi 2000).

But parallels among groups of migratory organisms break down when genetic mechanisms are considered. Until this point, the model has seemed robust across life forms moving cyclically to exploit resources distributed heterogeneously in space and time. However, the genetics of speciation in highly mobile organisms (or organisms with highly mobile gametes) can clearly be different. In birds, for example, hybridization is common and hybrids are commonly fertile (Grant and Grant 1997). Genetic incompatibilities are less likely than premating isolating mechanisms to cause reproductive isolation among birds (Price and Bouvier 2002, Price 2008). By contrast, Palumbi (1992, 1994) reviewed cases in which loci involved in egg–sperm or pollen–style interactions among free-spawning marine animals and high-dispersal plants (respectively) appeared to provide prezygotic isolating mechanisms that enabled speciation to occur despite a high propensity for gene flow. Genetic incompatibilities have also been proposed as an explanation for speciation in sympatric and migratory whales (Jarrell 1984).

The mobilization or availability of gametes while birds are still in migration may be functionally equivalent to wind-blown pollen in plants, but animals have behavioral mechanisms for gamete exchange (behavioral prezygotic isolating mechanisms). Mate choice among avian migrants could be highly assortative by being based on the timing (Hendry and Day 2005) of exhibition of male traits such as territorial defense and sustained song and displays. These time and energy investments would likely be disadvantageous to distantly breeding males if they were performed prior to a male's arrival at the end of a migratory journey. This postulated prezygotic isolating mechanism might be highly effective and be simply related to the loci under selection for timing and place of reproduction (which involve the timing of reproductive activity and the timing and direction of movement). This added mechanism (the spatiotemporal uses of territoriality, song, and displays) fits well with the theoretical addition of a sexually selected ornament that is conditionally expressed, which van Doorn et al. (2009) showed makes ecological speciation occur more easily.

Reinforcement.—Although in theory not necessary for speciation to occur under this model (cf. Doebeli and Dieckmann 2000, 2003, 2005), reinforcement, the evolution of prezygotic barriers to gene flow as a response to selection against hybrids (Futuyma 1998), may nevertheless occur. In modeling divergence and reinforcement under assortative mating, wherein assortment traits included timing of reproduction, Kirkpatrick (2000:1652) found that "a selectively neutral assortment trait will not necessarily diverge between hybridizing populations as an adaptation for decreasing gene flow." In other words, reinforcement is unlikely unless disruptive selection acts directly upon the trait. Among avian migrants this would seem to apply to sexually selected traits (discussed below) and to traits associated with ecological divergence in feeding behaviors and morphology if the disruptive selection promoting divergence is acting on traits associated with the timing of reproduction and the timing and direction of migration. Reinforcement may be highly effective in promoting assortative mating if hybrids of diverging populations are inferior in the timing of movement and breeding and in the direction of migratory movement (e.g., Helbig 1991, Kirkpatrick 2001). Matute (2010) demonstrated that reinforcement can be cryptic, involving postmating physiological differences in sperm processing, and that it can develop rapidly in *Drosophila*. Although the potential role for reinforcement here remains unknown, migrants may offer an important research area for the subject (Servedio and Noor 2003). Coyne and Orr (2004) reviewed reinforcement and offered the prediction that under reinforcement larger changes would be observed in female than in male behavior (or physiology or morphology) in mate selection. As Parker and Partridge (1998) and Coyne and Orr (2004) suggested, under reinforcement females should become choosier when confronted with two types of males, because the costs of reproduction are higher in females. Price (2008) reasoned that reinforcement is probably important in avian speciation, not through its frequent demonstration but rather because hybridization is rare in sympatric species.

Additional complexities.—Lineages that are recently derived through ecologically driven divergent selection, as proposed here, are particularly susceptible to reticulation (breakdown) when conditions change, because irreversible (i.e., genetic) isolating mechanisms do not yet exist (Muller 1942, Price 2008). This may be the mechanism behind Montgomery's rule, or why many of these lineages have not speciated. The process of heteropatric differentiation need not go to completion and produce species. Among organisms that engage in cyclic migration to exploit resource peaks that are spatiotemporally heterogeneous in distribution, it should be expected that longer-term climatic oscillations and environmental instabilities will frequently produce incomplete divergence. Such an outcome is both a theoretically and empirically important aspect of ecological divergence (Bolnick and Fitzpatrick 2007, Nosil et al. 2009b), and migrant taxa appear to be rich in examples (Table 1).

The progression of isolating mechanisms from reversible (assortative mating) to irreversible (genetic incompatibilities), coupled with the variability in speciation genetics among cyclic migrants (e.g., prezygotic versus postzygotic barriers being more important), precludes this model of heteropatric differentiation from including just a single isolating mechanism or population genetics model for speciation. More than one of each must occur among (but not necessarily within) diverging migratory lineages, and the simultaneous involvement of multiple mechanisms is possible. The inability of the model to focus on a single mechanism or population genetics model that must be operating for this type of speciation to occur is not a weakness of the model. Rather, it is an indication of the variation to be expected among the full organismic spectrum of migratory organisms and our still developing knowledge of the genetics of speciation. It is a puzzle to be worked out empirically among an array of organisms. Evolutionary biology has a successful tradition of initiating fruitful research by first outlining what seems to be occurring without knowing exactly how it occurs. For example, Darwin (1859) did not know about genetics, and founder-effect speciation, proposed more than half a century ago, remains a controversial topic that involves a series of potential mechanisms that have yet to be worked out (Coyne and Orr 2004, Templeton 2008). A review of all the possibilities is out of place here, but some research directions are suggested below.

Sexual Selection—Agent, Cue, or Needed at All?

Sexually selected traits such as male song and plumage characters are common among birds, and these traits can be important in mate choice among avian migrants. But has divergence among these migrants been stimulated by sexual selection, or instead has sexual selection trailed behind, perhaps providing a cue for mate choice among populations under disruptive selection from ecological factors such as the timing of reproduction, migratory condition, et cetera? Although the two may be tightly linked in avian migrants, I consider that the observed divergence would not occur without the stimulus of environmental heterogeneity promoting population divergence in the times and places of reproduction and movement. Sexual selection may then be an important cue, promoting increased assortative mating; environmental heterogeneity already promotes it through allochrony and allopatry.

Population-level traits among avian migrants within a biological species are often highly divergent in a suite of characters, such as the timing of reproduction, the timing and direction of migration, fat deposition (energetic strategies of movement and reproduction), and the timing of territorial displays. They are often comparatively less differentiated (if demonstrably so) in characters such as plumage and song (e.g., Pulido et al. 1996). Divergent selection on this suite of traits must be strong between migrant populations that breed allochronically and allopatrically, and these traits are not likely to be genetically linked with characters such as plumage and song. Among sedentary tropical birds there are many cases of the opposite condition: strong differences among subspecies in sexually selected characters but little or no differentiation in timing of reproduction. So we know what differentiation stimulated by sexual selection looks like phenotypically in birds, and this situation does not seem to be so prevalent at the time of speciation among migratory lineages. Thus, sexually selected traits, while undeniably important and often showing some divergence between populations and subspecies of migrants, in general seem to trail behind environmentally driven assortative traits among diverging migrant lineages. Using other evidence—the association of sexual dichromatism with geographic species diversity—Price (1998, 2008) came to a similar conclusion regarding the role of sexual selection in the ecological differentiation associated with adaptive radiations.

On the other hand, the environmental heterogeneity experienced and exploited by migrants offers an avenue for divergence that has been stimulated by sexual selection to continue, without being stopped by competitive exclusion (see also Arnegard and Kondrashov 2004). And, by enhancing assortative mating, the two types of selection might act very well in concert among organisms like birds in which mate choice through sexual selection occurs (cf. Doebeli and Dieckmann 2000, van Doorn et al. 2009). Female mate choice is likely to be an important source of assortative mating in diverging populations (Parker and Partridge 1998, Parker 2006). Biparental care of offspring is the predominant condition in birds. This entails a time commitment that by itself will select for assortative mating between diverging populations that have some degree of allochrony in their timing of reproduction—as long as the time difference is too short to enable individuals to exploit multiple resource peaks for reproduction. Thus, in birds, female mate choice could be as simple as an assessment of a male mate's likelihood of providing parental care or selection against pairings with males that do not provide such care. Less choosy females would experience lowered fitness through concomitantly lowered levels of offspring care. Given the prevalence of extrapair paternity in putatively monogamous avian systems, understanding the details of this will not come from study of pair bonding alone (Westneat and Stewart 2003). However, the importance of biparental care and female mate choice may provide a broad explanation of why pair-bond formation on nonbreeding grounds is an unusual condition among migrants. Even after insemination, though, female birds appear to have the ability to make cryptic choice (sperm selection) regarding the prezygotic outcome of matings (Birkhead et al. 2004; cf. Matute 2010). Postzygotic genetic incompatibilities preventing fertilization or causing the death of embryos seems less likely to be a factor in birds because these isolating mechanisms require a long time to develop (see Price and Bouvier 2002, Price 2008).

Thus, sexual selection is not necessary for the heteropatric model to work. However, the commonness with which avian song differs intraspecifically with environment (Price 2008), coupled with evidence of song divergence between subspecies of avian migrants associated with different environments and histories (e.g., Irwin and Irwin 2005, Ruegg et al. 2006), suggests that sexual selection may well be present in avian lineages that diverge under the heteropatric model. Collins et al. (2009) recently investigated components of song divergence in migratory and sedentary populations of Blackcaps (*Sylvia atricapilla*). The hypothesis that the shorter breeding seasons of migratory populations enhance sexual selection was supported by longer female-directed song components, whereas male–male competition seemed to drive song characteristics in sedentary populations. Sexual selection associated with female choice was stronger in migrants. Importantly, lineages that have diverged in sexually selected traits such as song are also likely to have diverged in their mating preferences for those traits (Price

2008). So, by acting synergistically, sexual selection may be an important additional dimension of divergence under this model in taxa such as birds. Again, however, disruptive selection caused by ecological heterogeneity should, in theory, be enough for divergence to occur. Even in birds, in which sexual selection is prevalent, mate selection among migrants based on sexually selected characters could be highly assortative simply by being based on the timing of the exhibition of traits such as song and territorial defense. In sum, reproductive isolation might develop between migratory populations entirely as a byproduct of ecological divergence, but sexual selection may be present and enhance such isolation.

COUNTERARGUMENTS

Allopatry remains a crucial component.—Yes, allopatry is a central component of the heteropatric model, but not in the traditional sense of spatial isolation over long periods. During the nonbreeding portion of the annual cycle considerable degrees of sympatry are common, and this overlap often extends into the reproductive periods of some populations. The limiting of gene flow in the heteropatric model is, of course, enhanced by allopatric breeding populations. However, such populations must first develop, despite increased movement and despite the greater opportunities for increased gene flow that seasonal sympatry offers, whether through the formation of nonbreeding pair bonds, behavioral switching, extrapair fertilizations, or other processes. Differentiating migratory lineages are unlikely to be squeezed into a conceptual box of strict allopatry. And, in this model of heteropatric differentiation, interbreeding is not restricted primarily by distance, which is a feature of both allopatric and parapatric models. I consider that individuals that occur together have the opportunity to reproduce. The fact that this seems to occur infrequently among differentiating lineages that have increased movement is not an affirmation of the allopatric component of the heteropatric model so much as illumination of the glaring historical omission of considering the sympatric aspect of these lineages.

To understand the process of differentiation that is occurring among seasonal migrants, we must learn how and why diverging populations and lineages do not reproduce when in sympatry (or the ways in which such crossings are disfavored). The heteropatric model opens the door to asking these important questions among organisms that are distributionally challenging and that are largely excluded from speciation theory despite ongoing differentiation in the face of increased movement.

Genetic sorting occurs on the breeding grounds.—That genetic sorting occurs on the breeding grounds seems like a convincing argument until it is realized how commonly higher-latitude migratory populations occur sympatrically with lower-latitude populations when the latter are breeding. Genetic sorting clearly occurs quite frequently in sympatry, in that individuals of different populations do not freely interbreed when in contact, despite ample opportunity, in many cases, to do so. Differentiation has obviously progressed in the face of such opportunities for gene flow. Given that male migrants are often found in a reproductively capable condition in migration (Quay 1986, 1989), that pair bonds might be formed on nonbreeding areas, and that the process of such differentiation had to begin with only very small differences in these traits, this is not a trivial observation. As the natural experiment in the Anatidae (waterfowl) shows, reproductive activities initiated when different breeding populations are in nonbreeding sympatry retards differentiation. Why is this rare among migratory birds? Apparently, some selective agent is generally preventing (1) nonbreeding pair bonding, (2) local females from selecting migrant males as mates, or (3) migrant females from storing sperm from local males, or (4) cryptic choice such as sperm selection may be occurring, or (5) selection operates against the hybrid offspring of such crosses. All of these may be involved.

Small population sizes may enable effective isolation.—It is conceivable that allopatry is effectively achieved because rarity causes isolation (and small effective population sizes) despite the distances that migrants travel. Very small populations of migrants may not meet with sufficient frequency to counter the differentiating effects of drift and selection, effectively producing the isolation required for allopatric speciation (i.e., peripatric speciation, a subclass of allopatric speciation; Coyne and Orr 2004). Such conditions could clearly facilitate differentiation, and this could presumably lead to speciation in migratory lineages. However, wholesale imposition of very low historical population sizes across the many and diverse lineages involved is as unsatisfactory as suggesting that they went through a nonmigratory or less dispersal-prone period. If this were a predominant mechanism for the observed differentiations, I would not expect to observe what appears to be a continuum across the levels of differentiation that presently occur among the world's migratory species that are common or abundant.

Is there one clear example?—As Coyne and Orr (2004:121) stated regarding parapatric speciation,

> if all phases of the process can be seen in nature, then it is reasonable to conclude that the entire process can occur in a single taxon. While we concur that this continuum supports the possibility of parapatric speciation, we cannot agree that it supports its likelihood.

Similarly, the model of heteropatric speciation rests on observations of differentiation that are coupled with increased movement of a cyclic nature that causes intermittent allopatry and sympatry. Nosil (2008) also observed that demonstrating speciation with gene flow is difficult. Migration and the distributional condition of heteropatry have been largely ignored in speciation theory, and so it remains to be explained how differentiation can proceed despite increased movement and substantial degrees of sympatry occurring among differentiating groups. I have attempted to do so here. Table 1, Figure 1, and the phenomenon of leapfrog migration suggest hundreds of likely examples of heteropatric speciation. Some possible examples are discussed below, but it remains for future research to provide unequivocal examples of this particular process of differentiation.

Some Predictions of the Model

Because this model of heteropatric speciation includes components of allopatry, sympatry, allochrony, and the possibility of nonzero effects of sexual selection, the series of predictions below are not all exclusive to it. However, they collectively establish the landscape upon which this model is likely to be most productively studied. Mainly I focus on how the heteropatric model makes predictions different from strictly allopatric processes, because historically that has been the dominant theory applied to migratory lineages.

Prediction 1.—The most obvious prediction made by the heteropatric model is that migratory lineages will, on average, tend to exhibit a different mode of speciation than sedentary lineages. With ecological factors promoting divergence, as suggested here, speciation among migratory lineages might, on average, occur more rapidly and under a much lower threshold of overall genomic differentiation than would occur through speciation in allopatry, wherein a more gradual accumulation of differences across many loci is probably more common. This prediction is not one of frequency (i.e., migratory lineages are not likely to experience more speciation events), but rather one of mode and rate. In the absence of strong divergent selection, mutation and drift would play a more important role early in the allopatric process than in the heteropatric model (these differences are considered in a broader context in Winker 2009). This prediction runs counter to the evidence presented by Peterson et al. (1999), which suggested that speciation is geographically and not ecologically based. But their analyses inappropriately excluded migratory lineages. Hendry et al. (2000, 2007) have shown that ecological speciation can appear fairly rapidly, and Schluter (2000) reviewed evidence for rapid speciation in some high-latitude fish lineages. The rapid anagenesis (increased specialization) that migratory populations of birds can exhibit (Berthold 2003, Bearhop et al. 2005) also suggests that cladogenesis (divergence from other lineages) could occur rapidly.

The reviews of Orr and Coyne (1992) and Orr (2001) suggested that not only different levels of genetic divergence but different patterns of divergence should be found between migratory versus sedentary taxon pairs at speciation. Perhaps the most obvious and testable is that there should be a greater discordance among gene genealogies between populations diverging through heteropatric speciation than between those diverging through strictly allopatric speciation (Hey 2006, Nosil 2008, Via and West 2008). Again, this is on average, because, as Gavrilets (2004) pointed out, allopatric speciation can also, in theory, occur rapidly when driven by selection. Recently, Nosil et al. (2009a), in focusing on divergent selection causing differentiation, termed this phenomenon "heterogeneous genomic divergence" and found that what they termed isolation-by-adaptation is not uncommon in present empirical data sets, lending further support to the broad occurrence of ecological speciation. The genomic architecture of this form of divergence is considered further below.

Prediction 2.—Gene flow between differentiated migrant populations should be low. This may seem an obvious and trivial prediction given that differentiation has progressed in so many migratory lineages, but its demonstration is important. The rapid divergence and subsequent isolation suggested here must be tested at subspecific levels, much as Buerkle (1999) demonstrated between Prairie Warbler subspecies in the southeastern United States, Kondo et al. (2008) showed in Baltimore and Black-backed orioles, and Pérez-Tris et al. (2004) showed in their Gibralter population of sedentary Blackcaps, which are synhiemic with other western migratory populations. Divergent selection need not result in reduced gene flow and the initiation of the speciation process (Crispo et al. 2006, Hendry et al. 2007). Testing this hypothesis should also include loci under selection (or linked to such).

Prediction 3.—The cyclic, spatiotemporal overlaps that occur among migrant populations constitute natural experiments in migrant differentiation. At least three areas of prediction and study suggest themselves. First, although in some cases it would appear that differentiation has not occurred, probably because of these overlaps, in other cases differentiation has progressed and at best may only have been slowed. The difference between the two outcomes must be related to the appearance and strengthening of disruptive selection between subspecies or populations. Obtaining estimates of evolutionary rates (Hendry and Kinnison 1999) among populations of congeneric species that exhibit different degrees of differentiation and conducting experimental crosses among such populations in captivity (e.g., Helbig 1991, Berthold 2003, Pulido 2007) could enable discovery of the importance and relative roles of the various selective factors that promote divergence. Nosil et al. (2009b) offered a series of additional means for testing the role of ecological factors in speciation, and they focused on whether stronger selection on a single trait versus selection on more than one trait (the "multifarious selection" hypothesis of Rice and Hostert 1993) might cause the difference between speciation being completed or not.

Second, even in apparently undifferentiated or clinally varying migrants, we are likely to find a condition that might be considered "temporal ring species," a sort of anagenesis (lineage specialization) wherein differentiation in timing of reproduction and timing and direction of movement has progressed sufficiently that hybrid crosses between individuals from populations at the distributional endpoints have low or no fitness. The ends of the "temporal ring" (a ring in which the "end" populations come together in time and space but are also geographically separated at other times in the cycle) can be sympatric during the nonbreeding season and into the reproductive season of the lower-latitude population, and allopatric during the reproductive period of the higher-latitude population.

Third, these natural experiments provide a rich and essentially unexplored area for studying character displacement and competition and their roles in ecological divergence. Migratory taxa present an opportunity to examine varying levels of biotic organization, from populations to species, alternating between sympatry and allopatry. Character displacement will likely be found to be common, but in characters not traditionally measured (see Schluter 2000), such as timing of reproduction, migratory direction and distance, et cetera.

Prediction 4.—This model has to work in both directions. It encompasses differentiation occurring when a population experiences selection associated with the exploitation of new, cyclically available ecological space (in spatial, temporal, and nature-of-resource dimensions, although the last seems uncommon in avian migrants). Thus, for example, I expect to see differentiation in populations that are exploiting new spatiotemporal breeding niches, whether this involves an increase in migratory tendencies (to occupy more distant breeding grounds) or, alternatively, a cessation of migration to exploit breeding opportunities present on wintering grounds. Similarly, specialization among cyclic migrants on the timing, distribution, and nature of nonbreeding resources could also promote divergence. Consequently, disruptive selection should be common at breeding-range contact zones between, for example, allohiemic populations, especially when the allohiemy involves different continents (i.e., when wintering grounds and the directions to them are fundamentally different). Helbig's (1991) experimental evidence suggests this, but the subject has only begun to be investigated (e.g., Bearhop et al. 2005). This condition, in which nonbreeding resource specializers are attempting to exploit the same or very similar breeding-resource peaks, may result in breeding-ground parapatry or perhaps even sympatry; this may be a common condition between African and Asian wintering populations on their breeding grounds in Eurasia (see maps in Moreau 1972, Irwin and Irwin 2005). Further studies of these tension zones (Barton and Hewitt 1985) or migratory divides (Salomonsen 1955; Bensch et al. 1999, 2009; Pérez-Tris et al. 2004; Bearhop et al. 2005; Irwin and Irwin 2005; Ruegg 2008; Toews and Irwin 2008) will be illuminating. Research on the heteropatric model, however, is better restricted to just one type of these contact zones, or migratory divides—those that are not simply the result of secondary contact of forms that have diverged in allopatry, although the same mechanisms may be involved in promoting reproductive isolation (see below).

Prediction 5.—The heteropatric model must work at very small spatiotemporal scales as well as large ones. It must work to explain the appearance of migration itself from sedentary ancestors and differentiation occurring, for example, among aquatic organisms in such cyclic environments as water columns. Although the heteropatric model is based on observations at larger scales, its robustness depends on its being applicable wherever cyclic movements and heteropatric conditions are accompanied by evolutionary differentiation. As the coefficients of space and time become very small, this model may become inseparable from sympatric speciation models in the initial differentiation, but the occurrence of heteropatry should greatly enhance the probability of this differentiation proceeding to speciation. Garant et al. (2005) found that nonrandom dispersal alone could foster differentiation at small scales in a nonmigratory bird, and modeling demonstrates that adding a spatial component to sympatric models increases the likelihood of differentiation—although long-distance movements counter differentiation under these modeled conditions (Doebeli and Dieckmann 2003). Differentiation occurring with increased movement and heteropatry suggests that the relatively long-distance movements of cyclic migration have not yet been adequately incorporated into these mathematical models at these scales.

Prediction 6.—Finally, in considering mechanisms that initiate the process and that enable differentiation to progress under this model, it is possible that developmental (or phenotypic) plasticity and variation in gene expression are more important than mutation, at least in early phases. Subsequently, selection (which acts on the phenotype) causes gene frequency changes through genetic accommodation that are associated with the favored traits (Berthold 2003; Price et al. 2003; Rappole et al. 2003; West-Eberhard 2003, 2005). Under this scenario, cyclic behaviors are induced by environmental inputs (environmental induction; West-Eberhard 2003, 2005). This results in a local behavioral response—increased movement with a go-and-return component—to exploit local (i.e., nearby) resource peaks that are different in space and time from those available to individuals that do not undertake such movements. If favorable, these new phenotypes result in an increased frequency of genes associated with the new behavioral phenotype(s). Then, through such genetic accommodation, genes that regulate the associated behaviors and developmental thresholds (e.g., in timing of gonadal growth and recrudescence, fattening, molt, territorial behavior, mate selection, and song) "lock in" an endogenous direction (anagenesis) to cyclic migration and the process of differentiation (cladogenesis) in relation to subpopulations that do not exhibit such movements (or exhibit the traits on a different evolutionary trajectory). In such cases, finding a genetic signature of divergence early in the process could prove quite challenging (Rappole et al. 2003).

In sum, these predictions raise questions that bring migratory taxa to the frontiers of modern evolutionary biology and require the integration of fields such as behavior, developmental biology, and genomics to answer. Exciting developments are being made in these areas (e.g., Berthold 2003, Bearhop et al. 2005, Kondo et al. 2008), but their interdisciplinary integration to understand differentiation and speciation in migratory lineages is only beginning. As Butlin et al. (2008) observed, lineages available for study today represent different stages in the speciation process. And even if the past or future of diverging lineages are unknown, these lineages can inform us about how selection and genetics result in different levels of reproductive isolation. Among birds, divergence is associated with the advent of cyclic migration from population levels through and beyond speciation. The many lineages that together exhibit this spectrum of divergence are rich ground for the study of how divergence and reproductive isolation develop despite the increased propensity for gene flow that cyclic migration causes.

FUTURE DIRECTIONS

I have presented a conceptual model based on observations of differentiation that occur with the advent of increased movement due to cyclic migration that causes individuals from separate breeding populations to occur across the distributional spectrum, from sympatry to allopatry. Three big questions remain.

(1) Does heteropatric speciation occur? Inference suggests that it does, but clear demonstrations are required. Possible candidates that have begun to be studied in detail include lineages studied by Helbig et al. (1996; the Common Chiffchaff subspecies *Phylloscopus collybita abietinus* vs. *P. c. brevirostris/caucasicus*; as highlighted in Helbig 2003), Buerkle (1999), Yosef et al. (2000; as noted in Helbig 2003), Pérez-Tris et al. (2004; the synhiemic Gibralter population), Bearhop et al. (2005), and Kondo et al. (2008).

(2) How does heteropatric speciation occur? The model conditions given above provide suggestions; these also require demonstration.

(3) How often does heteropatric speciation occur? Divergence with increased cyclic movement is common within species; it remains unclear how often heteropatric differentiation has resulted in speciation. Large species flocks or adaptive radiations stimulated by cyclic migration as a key innovation may be unlikely or rare, but smaller species clusters with a migratory ancestor may prove to be common.

In migrant birds, divergence can be seen in lineages as closely related as populations and as distantly related as species and even genera. However, although I am using multiple levels of divergence to infer that the heteropatric speciation process occurs—because divergence can be seen proceeding in the presence of cyclic migration—I do not think that the process itself can be effectively studied across these many levels. The reason is simple: after speciation, genotypic divergence between two lineages is expected to inexorably increase, whereas how phenotypic divergence will progress cannot be predicted, either in direction or in magnitude (Fig. 2). Thus, the passage of time inevitably inflates the inferred importance of time on the process of speciation (genetic distance is usually used as a proxy for measuring time since divergence). This biases our ability to deduce the importance of divergent selection associated with that process (Fig. 2); Rundell and Price (2009) have recently considered this in more detail. As a consequence, the farther lineages get from speciation, the less confidence can be placed in reconstructions of the role of ecological factors in the speciation process. Via and West (2008) approached this from a different direction (genomics) to reach a similar conclusion. This is one reason why I have given subspecies such prominence.

Research on this heteropatric speciation model and its predictions will need to recognize the

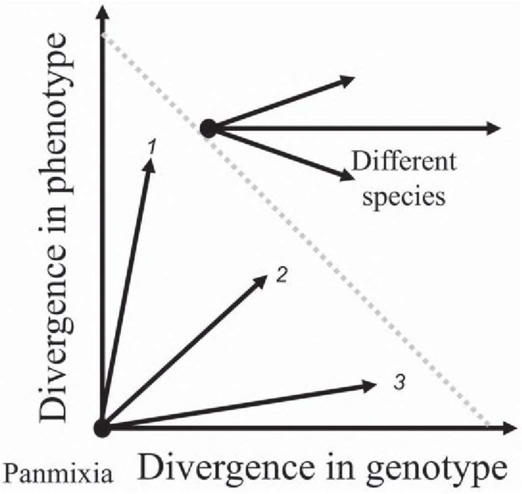

FIG. 2. Divergence process space, showing for heuristic value two axes of divergence, phenotypic (probably mostly adaptive) and genotypic (probably mostly neutral in today's data sets; Winker 2009). Different routes to speciation are possible, operating below the dashed line demarcating different species (arrows 1–3): route 1 would be predicted by heteropatric speciation, whereas route 3 would be expected of populations diverging without strong divergent selection (e.g., in allopatric populations that occupy similar environments). Route 2 indicates the route in which genotypic and phenotypic divergence are coupled (which seemed unlikely in Winker 2009). The triplet of arrows at the top indicates how, once diverging populations have achieved reproductive isolation and become species, movement on the axis of genotypic divergence is inexorably positive, whereas movement on the phenotypic axis is not readily predictable. Thus, the passage of time between populations that have become species inevitably increases the apparent importance of time (usually determined using genetic divergence estimates as proxy) and diminishes the apparent importance of divergent selection on phenotype in the divergence processes that lead up to speciation. This makes it increasingly difficult, following speciation, to determine the nature and importance of divergent selection on phenotype in causing that speciation. For research on heteropatric speciation (and other types of ecological speciation), this bias is best overcome by focusing on populations before or very near the time they have become full species.

limitations of traditional phenotypic and genotypic approaches. For example, retention of ancestral genetic polymorphisms, essentially a record of deeper historical gene flow, could cloud contemporary genetic processes (e.g., Oyler-McCance et al. 2010, Pruett and Winker 2010). And subspecies, which are based on phenotypic characters whose genetic bases are usually not understood, do not necessarily represent evolutionary units (Mayr 1963). Subspecies have been very important in developing an understanding of the processes of evolution and speciation (Mayr 1963, Zink and Remsen 1986, Winker 2010), but their utility for further study of the model proposed here is limited. The type of geographically partitioned phenotypic variation that subspecies represent typically does not include characters important in the heteropatric model (e.g., timing of behavioral or physiological characteristics). However, although seldom investigated in detail, the phenotypic variations upon which subspecific designations are based can reflect local adaptation (e.g., Hoekstra et al. 2006, Mumme et al. 2006). Thus, the occurrence among migrants of geographically structured phenotypes—in many cases likely to be adaptive clusters—in the face of their increased movement provides heuristic value in suggesting taxa for research on this model.

Behavioral studies of diverging populations when and where they are in contact (in breeding and nonbreeding areas) will be useful for determining the nature of isolating mechanisms and the ecological dimensions of divergent selection operating between them. How nonbreeding resources are used between synhiemic diverging lineages will be quite interesting (e.g., Pérez-Tris and Tellería 2002, Tellería and Pérez-Tris 2004). Mate-choice experiments might prove useful in some taxa (Hendry et al. 2007), but in migratory birds these will be difficult. Even the widely used song-playback method of determining responses between populations usually neglects the critical factor of female choice (though see Patten et al. 2004); whether males respond positively or negatively to song playback (which could have a basis in resource competition), females may respond oppositely, and this is usually difficult to determine.

Modeling and further studying the distributions of these organisms has to include nonbreeding distributions. Considering breeding ranges alone is unlikely to be effective in understanding this speciation model. What happens and what does not happen (e.g., mate choice) when and where diverging populations occur in the nonbreeding parts of the cyclic movements (of one or both populations) are fundamentally important. A full accounting of the cyclic distributions is required. However, including nonbreeding distributions in models of historical ranges may prove unsatisfying, particularly as the time dimension becomes deep. The generally shallower ecological gradients of change that occurred across evolutionary time at lower latitudes will likely result in model space that is too broad to be definitive. Add to this the sheer mobility of these animals, and determining where and when they occurred historically becomes highly problematic (and distributions of individuals in migration are nearly always excluded). Often it seems that these organisms just do not sit still long enough to confidently follow a case from beginning to end. Thus, I largely agree with Butlin et al. (2008:3005) that we can become overly focused on distributional reconstructions or categorizations and that

> It is likely to be most productive to focus on the current balance between selection and gene flow rather than trying to establish how divergence began at an unknown time in the past or how it will progress in the future.

Here, this brings the genetics of divergence and reproductive isolation to the fore in the context of present, heteropatric distributional conditions.

Genetics.—Geographic variation in genotype and phenotype can easily be decoupled at the intraspecific scale because of temporal differences in the accumulation of changes exhibited (or measured; Winker 2009). Differences in the patterns of geographic variation revealed by traditional phenotypic and genotypic data sets are therefore to be expected. In other words, the accumulation of change when stabilizing or divergent selection affects phenotype through a small portion of the genome is likely to occur on a different time scale than the accumulation of change through the putatively neutral genetic divergence that makes up most of the variation in genetic data from portions of the genome not under such selection (the majority of genetic data presently used in the study of geographic variation; consider route 1 vs. route 3 in Fig. 2). Additionally, rates of introgression of mitochondrial and nuclear DNA between hybridizing lineages can be discordant (Coyne and Orr

2004). In short, the genetic markers that presently dominate the study of phylogeography, while useful for initial inference, are not likely to be the most useful for studying speciation under the heteropatric model.

It seems unlikely that heteropatric differentiation will occur through the fixation of new mutations; instead, it is likely to develop from standing genetic variation (Rice and Hostert 1993, Noor and Coyne 2006, Pulido 2007, Rice 2008). Studies of the genetic bases for phenotypic differentiations such as the timing and direction of migration or the timing of reproduction (Hendry and Day 2005, O'Malley et al. 2007) can reveal the genetic bases of divergent adaptations in migratory forms. But relatively little is known about the genomics and developmental attributes of migratory traits (e.g., Alerstam et al. 2003, Rappole et al. 2003, van Noordwijk et al. 2006, Pulido 2007, Rice 2008). Candidate genes remain few, and the genetic regulation of migratory traits remains largely uninvestigated. Nevertheless, it will be important to focus on loci influenced by selection, rather than on the putatively neutral genetic attributes that are presently common in phylogeography and population genetics. What is found will almost certainly be complex. First, for example, obligate migration arose independently among many lineages, even in birds—broadly at the order and family levels, but even within genera (e.g., Helbig 2003, Winker and Pruett 2006). If even comparatively simple traits such as pelage melanism can have different genetic bases in different populations of the Rock Pocket Mouse (*Chaetodipus intermedius*; Hoekstra and Nachman 2003), then it is to be expected that cyclic migration will be genetically complex. Second, even in birds, variation in factors such as reliance on different navigation systems and nocturnal versus diurnal migration suggests that the genetic bases of migration will differ among migrant lineages (e.g., Alerstam 2006). Third, again even in birds, evidence suggests that migration as a trait complex can have both strong and weak genetic correlations among associated traits (van Noordwijk et al. 2006, Pulido 2007). Nevertheless, modularity (West-Eberhard 2003, Rice 2008) in at least some traits should be expected and sought within, for example, family- or order-level groups of migratory lineages.

Methods to identify loci under selection (or linked to such) through population genomic scans such as amplified fragment-length polymorphisms are proving invaluable for studying the effects of divergent selection on the genomes of nonmodel organisms (e.g., Beaumont and Balding 2004, Nosil et al. 2009a). There are several weaknesses with such population genomic scans, however (Stinchcombe and Hoekstra 2008), and, regardless of approach, care must be taken to avoid overly simplistic analyses and interpretations, such as in conducting statistical tests with unrealistic assumptions and giving inadequate consideration to false positives when seeking evidence of adaptive genetic divergence (Benjamini and Hochberg 1995; Beaumont and Balding 2004; Hughes 2007, 2008; Nosil et al. 2009a). Taking the next step and mapping population traits under selection to specific locations in the genome and identifying loci influenced by selection is beginning to occur (e.g., Rogers and Bernatchez 2005, 2007; Via and West 2008). Ellegren and Sheldon (2008) and Stinchcombe and Hoekstra (2008) have advocated combining fields such as population genomics and quantitative genetics to determine the molecular bases of adaptive traits in model and nonmodel organisms.

As loci under selection are identified and sequence data become available, our analytical power over these questions grows considerably, particularly when placed into population-genetics and multilineage comparative frameworks (e.g., Kuhner 2009; McCracken et al. 2009a, b). A comparative approach that contrasts the genetics of populations within an environment with that of populations between environments will be especially useful, within and among species (Campbell and Bernatchez 2004; Rogers and Bernatchez 2005; Hendry et al. 2007; Via and West 2008; McCracken et al. 2009a, b; Nosil et al. 2009a). Whether (or when) genes involved in migratory traits exhibit protein-coding or *cis*-regulatory differences between diverging populations will be of considerable interest (Stern and Orgogozo 2008). What is known so far of migration in birds suggests that gene expression and regulation will be more important (Rappole et al. 2003, Pulido 2007), but a lot remains to be learned.

How low levels of gene flow can fail to cause diverging lineages to reticulate (break down) is an ongoing issue in speciation research (Noor and Coyne 2006). Hey (2006) suggested that when there is gene flow between diverging populations, the genes related to divergence will likely be located where recombination is restricted. Via and West (2008) called this phenomenon the "genetic mosaic of speciation" and found that divergence hitchhiking can occur for a considerable distance around quantitative trait loci. Nosil et al. (2009a) termed such occurrences "genomic islands" of divergence and provided a visual model (their fig. 4). In addition to this, Noor and Coyne (2006) considered two more ways in which divergence can continue despite introgression: (1) introgression occurs, but it is genomically small (e.g., in mtDNA only); or (2) introgression is restricted to alleles that produce increased reproductive isolation (e.g., females choose mates like their fathers), further decreasing gene flow. All three of these might occur under the heteropatric model. An interesting question is whether the relatively low levels of morphological divergence that seem common among diverging migratory lineages might be due to low levels of gene flow and the continued spread of advantageous alleles holding lineages together in "cryptic diversity" morphological space (e.g., Morjan and Rieseberg 2004). Study of populations likely to be diverging under the heteropatric model will advance our understanding of the genetic landscape of speciation with gene flow.

Perhaps the closest thing migration research has to model organisms are European warbler species in the family Sylviidae, and studies on various migratory traits in these taxa have provided an excellent series of reports on genetics, heritability, and environmental effects in avian migration (Berthold 2003). In captivity, migrants are amenable to experimental approaches such as common gardens, cross-population interbreeding, and quantitative genetics. As van Noordwijk et al. (2006) pointed out, reaction-norm approaches in such studies, which focus on gene-by-environment interactions, can prove very useful. The genomics of speciation and of migration represent areas in which rapid development is to be expected. We are on the threshold of learning about genomic architecture and the influences of factors such as copy number variation (Perry et al. 2007, Conrad et al. 2010), chromosomal inversions (Noor et al. 2001, Rieseberg 2001), expression and regulation (Abzhanov et al. 2004, Kudla et al. 2009), and DNA topography (Parker et al. 2009) on migratory traits. As more is learned about the genomics of migration and association between traits, integration with population, molecular, and developmental biology will dramatically improve our abilities to test hypotheses stemming from this and other models of ecological speciation.

Migratory divides.—East–west differentiation in migratory lineages occurs across and within the world's major migration systems. However, the presence of this phenomenon does not necessarily indicate that differentiation is occurring through the processes of the heteropatric model proposed here. Some of this differentiation is probably due to divergence in allopatry with subsequently renewed contact of breeding ranges (although persistence of this condition would likely require divergent selection; e.g., Irwin 2002). This is why I have focused on leapfrog and other north–south differentiation, which is generally incompatible with allopatric scenarios for divergence. It seems unlikely, however, that all east–west differentiation, particularly that occurring within migration systems, developed under traditional allopatric models, given the scale of migrant movements (with the correspondingly high propensity for gene flow) and the likelihood of some migratory divides developing when new nonbreeding resources become exploited by different populations that occupy a continuous breeding range. For example, Bearhop et al. (2005) found that a migratory divide formed within just 50 years of the establishment of a new, allohiemic wintering population, resulting in not only a migratory divide but also assortative mating, probably driven by selection driving the timing of reproduction. Thus, under conditions in which continuously distributed breeding populations subsequently develop allohiemy, the geographic directions of divergences become unimportant, and such cases would be similar to leapfrog divergence, with the heteropatric model for differentiation proposed here being fully applicable.

Heteropatric differentiation involves many of the same attributes that a series of studies have proposed as important for determining the outcome of allopatric and parapatric speciation processes (e.g., Irwin and Irwin 2005, Ruegg 2008, Bensch et al. 2009, Toews and Irwin 2009). From this work it seems clear that migratory traits (e.g., routes, timing, etc.) can be important in speciation in migratory lineages. The most important difference between these studies and what I am proposing lies in the distributional origins of divergence (i.e., involving sympatry as well as allopatry or parapatry).

Although many of the predictions made above may be more readily investigated where breeding ranges come into contact, the processes in these cyclic systems are decidedly not restricted to cases in which diverging populations happen to have contact zones where their timing and location of reproduction coincide. Nonbreeding distributions, especially conditions of allohiemy, need to be fully incorporated into research on this subject. More attention also needs to be paid to the largely neglected but rather common situations in which reproduction in one diverging population occurs while it is in sympatry with individuals of another.

Mathematical models.—I have not provided mathematical models or simulations of this verbal model of heteropatric speciation for two reasons. First, a robust empirical development of the conceptual basis is more important at this early stage of the concept. Second, an equally robust mathematical approach would be difficult to debut simultaneously, and to my knowledge no major speciation model has had a robust mathematical basis at its outset. Mathematical models tend to require oversimplifications of real-world phenomena to be tractable, usually leading to many trials, errors, and modifications before becoming accepted as likely to be occurring in natural populations. I did not want to risk having the heteropatric speciation concept dismissed because an immature mathematical model is found not to be very applicable in natural populations. The complexity of the topic puts a robust mathematical approach outside the scope of this monograph and will likely require the type of collaborations that are currently producing the mathematical models that I think are most relevant (e.g., Dieckmann and Doebeli 1999, Kondrashov and Kondrashov 1999, and especially van Doorn et al. 2009).

Conclusions

Differentiation in migratory lineages can be affected by many factors, reflecting responses to different degrees of sympatry, isolation, and selection. However, any general summary of the interplay between cyclic migration and differentiation has to include acceptance that what occurs today—large numbers of migrants moving relatively long distances to exploit cyclically available resources—is likely to represent the historical condition. This process cannot be stopped to accommodate a speciation model unable to move appreciably from a core of isolationism.

Differentiation clearly proceeds in the face of the increased movements of cyclic migration and often produces patterns, such as leapfrog migration, that are dubiously attributable to strictly allopatric processes. Moreover, the evolution of migration appears to have stimulated differentiation in some groups, presumably by having opened new environments to an ancestral form. The fact that increased cyclic movement can stimulate differentiation is also incompatible with a strictly allopatric model.

Sympatric speciation theory can help explain differentiation that occurs in the context of cyclic migration. But, with both allopatric and sympatric distributions occurring during these migrations (= heteropatry), a new model is warranted that contains aspects of both ends of this distributional continuum and the increased movement caused by this life-history trait. Current parapatric models are also inappropriate for this type of differentiation, for reasons of distribution, natural history, and increased movement. However, insights from all three model groups are valuable. Allopatric speciation seems to be the most common mode of speciation among essentially sedentary lineages, and allopatry and allochrony remain important components of this heteropatric model. But beneath the somewhat confusing factors of extensive organismal movement and mixed distributional conditions, migratory lineages provide a rich, largely unexplored succession of natural experiments in differentiation and speciation.

Acknowledgments

I thank T. Price, J. Avise, K. Scribner, J. Rappole, M. Morrison, the late Ernst Mayr, and several anonymous reviewers for helpful comments on earlier drafts, and the late Mario Ramos for helpful discussions.

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