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Ring species as bridges between microevolution and speciation

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Abstract

A demonstration of how small changes can lead to species-level differences is provided by ring species, in which two reproductively isolated forms are connected by a chain of intermediate populations. We review proposed cases of ring species and the insights they provide into speciation. Ring species have been viewed both as illustrations of the history of divergence of two species from their common ancestor and as demonstrations that speciation can occur in spite of gene flow between the diverging forms. Theoretical models predict that speciation with gene flow can occur when there is divergent ecological selection, and geographical differentiation increases the likelihood of speciation. Thus ring species are ideal systems for research into the role of both ecological and geographical differentiation in speciation, but few examples have been studied in detail. The Greenish warbler is a ring species in which two northward expansions around the Tibetan plateau have been accompanied by parallel evolution in morphology, ecology, and song length and complexity. However, songs have diverged in structure, resulting in a lack of recognition where the reproductively isolated forms come into contact in Siberia. Our analysis suggests that these differences could have arisen even with gene flow, and that parallel rather than divergent ecological changes have led to divergence in sexually selected traits and subsequent speciation.

> "Those forms which possess in some considerable degree the character of species, but which are so closely similar to some other forms, or are so closely linked to them by intermediate gradations, that naturalists do not like to rank them as distinct species, are in several respects the most important to us".
>
> Darwin, 1859, p. 47

Introduction

Almost a century ago, Stejneger in Jordan (1905) conceptualized the possibility that a single species might expand along two pathways around a geographic barrier with the terminal forms gradually diverging and eventually behaving as two species when they meet on the other side. This would result in a complete ring of populations with only a single species boundary. Mayr (1942) called such 'circular overlaps' the 'perfect demonstration of speciation', and he used them as prime examples of geographic speciation. Now called 'ring species' (Cain, 1954), such systems have been of tremendous interest to evolutionary biologists and systematists alike. But although the concept of ring species has provoked much thought, there is also confusion with respect to what exactly ring species are and what they teach us about evolution.

Two potential characteristics of ring species have caused them to be of interest to students of speciation. First, the history of species' formation can be traced through the geographical variation connecting the reproductively isolated forms, demonstrating how microevolutionary changes can accumulate into the differences between species. Such a historical approach has been used recently to study divergence of traits in *Ensatina* salamanders (Stebbins, 1949;

Brown, 1974; Wake & Yanev, 1986; Moritz, Schneider & Wake, 1992; Jackman & Wake, 1994; Wake & Schneider, 1998) and the Greenish warbler, *Phylloscopus trochiloides* (Ticehurst, 1938; Irwin, 2000; Irwin, Bensch & Price, 2001). Second, ring species might provide a demonstration of the way geographical differentiation to the level of species can occur in the face of ongoing gene flow. Biologists have differed in the importance they place on these two potential characteristics of ring species, and hence proposed ring species come in wide variety. The differing emphasis on these two characteristics leads to differences in opinion about whether specific cases qualify as ring species and what ring species teach us about speciation. In this paper we review the history of the ring species concept, review the way in which gene flow and selection are thought to interact in classic models of speciation, summarize the proposed cases of ring species, and conclude with a closer look at the Greenish warbler ring and the insights into speciation it provides.

History, gene flow, and the ring species concept

The debate over whether ring species display the history of divergence or demonstrate speciation with gene flow, or both, can be traced back to early writings on ring species. Although Stejneger in Jordan (1905) emphasized historical divergence and did not mention the necessity of gene flow connecting neighboring populations in a ring species, Mayr (1942) originally incorporated both of these ideas into his concept of circular overlaps. He stated that they were cases of 'speciation by force of distance', implying that divergence occurred between the terminal forms even though gene flow connected them around the ring. But his discussions of specific cases generally emphasized how circular overlaps could be used to reconstruct the history of speciation. Indeed, many of his examples (Mayr, 1942, 1963) were cases in which a mainland species has colonized an oceanic island twice, and the two island forms coexist without interbreeding. In such situations current gene flow through the mainland form is unlikely to play a role. Later Mayr (1970, p. 320) completely abandoned the role of gene flow in his concept of circular overlaps, stating that

> "Speciation by distance is a process that seems far less well established now than it did 20 years ago.... [Evidence for speciation by distance] is singularly missing in all species with a contiguous distribution of populations. Not even the cases of circular overlap, often cited as evidence, are conclusive. There are major gaps in nearly all of these chains of populations or at least evidence for the former existence of such gaps".

Although abandoning the gene flow concept, Mayr (1970, p. 292–293) continued to emphasize the way that circular overlaps demonstrate history:

> "It is immaterial whether these instances of circular overlap present themselves in the simplest and most diagrammatic manner or whether they are somewhat more complicated.... In either case the process of geographic speciation can be followed step by step. A more dramatic demonstration of geographic speciation than cases of circular overlap cannot be imagined".

At the same time that Mayr was downplaying the presence of gene flow in ring species, Dobzhansky was emphasizing it, both in his own work on cases of circular overlaps in *Drosophila paulistorum* (Dobzhansky & Spassky, 1959; Dobzhansky et al., 1964; Dobzhansky & Pavlovsky, 1967) and in his discussions of the *Ensatina* complex (Dobzhansky, 1958). In these cases he stressed that the chain of populations was a 'genetic bridge' that enabled genes to be exchanged between forms that are otherwise reproductively isolated. However, the 'bridges' in the *Drosophila paulistorum* complex were determined in laboratory breeding experiments using crosses between populations that were separated by large distances (Figure 1). The various forms of *Drosophila paulistorum* do not appear to form any sort of continuous ring geographically. In several localities, two groups of *D. paulistorum* occur sympatrically without interbreeding, although each group can interbreed in the lab with a 'transitional' race that occurs elsewhere. But even while Dobzhansky stressed the importance of gene flow in circular overlaps, he acknowledged that in this case 'it is questionable whether [gene flow] is actually taking place' (Dobzhansky et al., 1964).

The recent debate over one of the most intensively studied ring species, the *Ensatina eschscholtzii* salamanders along the west coast of North America (Highton, 1998; Wake & Schneider, 1998), has also focused on the importance of gene flow to the ring species concept. *Ensatina* salamanders have apparently expanded from their ancestral range in northern California southward along two mountain ranges that

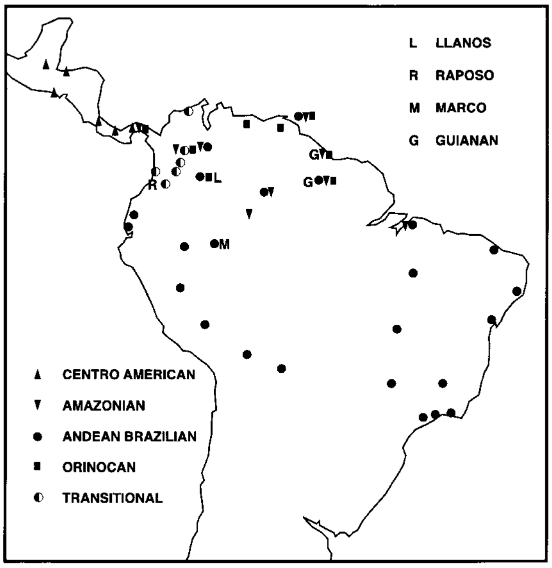

Figure 1. The geographic distribution of incipient species of the *Drosophila paulistorum* complex, redrawn from Dobzhansky and Pavlovsky (1967). Symbols correspond to 8 strains that are reproductively isolated from one another, and one Transitional race that can sometimes successfully interbreed with more than one of the other strains in laboratory experiments.

are separated by the Central Valley of California (Figure 2; Stebbins, 1949; Wake & Schneider, 1998). The two lineages now meet in southern California, where they differ in appearance and usually fail to interbreed. Dobzhansky (1958) proposed that gene flow around the ring slowed divergence of the terminal forms. Wake and Yanev (1986) investigated this possibility using molecular markers and concluded that gene flow is extremely limited in several areas around the ring. However, they continued to argue for its status as a ring species, emphasizing the reproductively isolated forms in the south and the general gradient in morphological traits through the chain of populations to the north (Wake & Yanev, 1986; Moritz, Schneider & Wake, 1992; Jackman & Wake, 1994; Wake & Schneider, 1998). Highton (1998) argued against ring species status and suggested that *Ensatina* should properly be treated as possibly 11 distinct species, based on evidence of breaks in current gene flow around the ring. These opinions resulted from differing concepts of ring species. Highton (1998) primarily emphasized the necessity of smooth gene flow through the chain of populations whereas Wake and Schneider (1998), like Stebbins (1949) before them, emphasized the history of range expansion and gradual divergence, placing little importance on contemporary gene flow throughout the entire ring. In conclusion, ring species have almost always been viewed as illustrating the history of speciation, but only sometimes has gene flow been considered an essential characteristic of ring species.

Gene flow and speciation

The extent to which gene flow prevents population differentiation is pivotal to theories of speciation (Ehrlich & Raven, 1969; Endler, 1977; Futuyma & Mayer, 1980; Slatkin, 1987). Genetic exchange between populations must slow down their rate of divergence. The longstanding question has been: by how much? As we have noted, one interest in ring species has been because they may demonstrate that speciation can occur in the presence of some gene flow (parapatric speciation; Gavrilets, Li & Vose, 1998; Gavrilets, 2000). In fact, recent interest has been focused more on the possibility that speciation can occur despite very large amounts of gene flow (sympatric speciation: Kondrashov, Yampolsky & Shabalina, 1998; Dieckmann & Doebeli, 1999; Kondrashov & Kondrashov, 1999). The impact of gene flow on population differentiation depends on whether divergence between populations is attributed to local adaptation, drift, or the initial fixation of mutations that are advantageous throughout the species range.

Recent models of speciation have emphasized the importance of local adaptation as a process which can oppose gene flow, resulting in quite rapid population divergence to the level of full species (Rice & Hostert, 1993; Gavrilets, 2000; Johannesson, 2001). This 'divergence with gene flow' model is currently receiving much attention (e.g., Smith et al., 1997; Schneider et al., 1999; Danley et al., 2000; Smith, Schneider & Holder, 2001). In the extreme of complete sympatry, gene flow between populations can be eliminated if selection is very strong, in which case speciation is likely to be very rapid (Kondrashov, Yampolsky & Shabalina, 1998). Although sympatric speciation is rare (Futuyma & Mayer, 1980; Coyne & Price, 2000) there are a few cases where it may have occurred in competitor- free, resource-diverse environments (e.g., Schliewen, Tautz & Pääbo, 1994; Dieckmann & Doebeli, 1999; Filchak, Roethele & Feder, 2000; Wilson, Noack-Kunnmann & Meyer, 2000). Divergent selection pressures between populations can also lead to the divergence of sexually selected traits, for example because different sens-

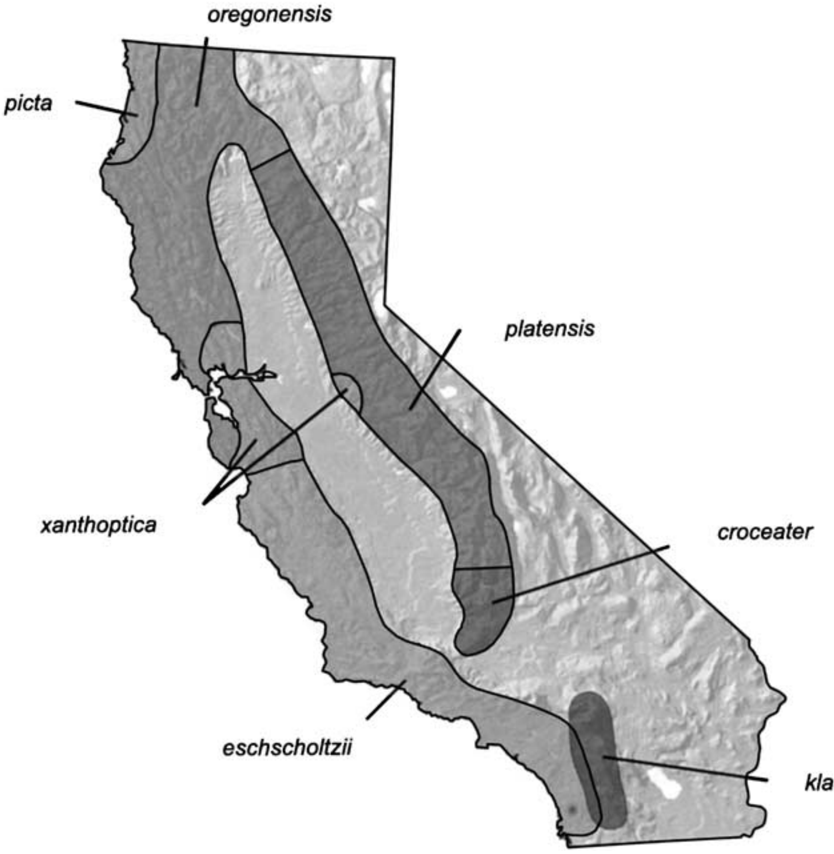

Figure 2. Map of California showing the distribution of seven subspecies of the *Ensatina eschscholtzii* salamander complex, redrawn from Jackman and Wake (1994). There is apparent intergradation between subspecies around the ring, except in two places where divergent forms have come into secondary contact. In the foothills of the Sierra Nevada *E. e. xanthoptica* and *E. e. platensis* meet in a narrow hybrid zone where parental forms predominate. In the mountains of southern California *E. e. eschscholtzii* and *E. e. klauberi* coexist as separate species, where they hybridize rarely. These two southern forms are strikingly different in coloration, and morphology changes gradually through the ring of populations to the north.

ory modalities are favored in different environments (Endler, 1992; Schluter & Price, 1993).

An alternative model of speciation is based on geographical isolation. Gulick (1890a) was the first to suggest that population differentiation and speciation may occur even in the absence of divergent selection pressures: 'I have accumulated a large body of facts indicating that separated fragments of species, though exposed to the same environment, will in time become divergent'. Divergence may be due to random drift (Gavrilets, 2000), or to an interaction of random processes with selection (Gulick, 1905; Lande, 1981; Orr, 1995). Population divergence in the absence of selection favoring local adaptation may be greatly impeded by migration. This will be particularly true if a new mutation that becomes established in one population is also favored in other populations. In this case, even a trickle of gene flow will result in rapid spread of the mutant form throughout the species range (Barton, 1979). A possible example of this in progress is the spread of a male secondary sexual trait (the color of the collar) across a hybrid zone of two species of manakins, *Manacus vitellinus* and *M. candei* in Panama (Parsons, Olson & Braun, 1993).

An almost complete barrier to gene flow is required for an unconditionally favored mutant to remain confined to one population (Barton, 1979). The only way for population differentiation to build up to the level of reproductive incompatibility is by the spread of additional mutations that are favored on one genetic background but not another. Incompatibility results if these additional mutants are maladaptive in other populations with different genetic backgrounds (Muller, 1942; Orr, 1995). Gulick (1890b) proposed interactions between the sexes (including sexual selection) as one mechanism whereby differentiation could be achieved in this model. He noted that 'adjustment of the male and female elements to each other are liable to become slightly divergent, producing mutual infertility'. The idea seems to contain the elements of the recently espoused sexual conflict models of speciation (Rice, 1998, 2000; Arnqvist et al., 2000). In these models males evolve attributes that make them more successful at fertilization, and if these attributes are deleterious to females, females evolve resistance to them. The spread of two new mutations in one population (male trait and female resistance) at least gives the potential for reproductive incompatibility between this population and others in which neither mutation has become established.

We conclude that the role of gene flow in preventing differentiation of the terminal forms of a ring species should be highly dependent on whether initial substitutions are favored everywhere or only in parts of the species range. In the former, a small amount of gene flow may be sufficient to homogenize the species (Barton, 1979), while in the latter, even large amounts of gene flow may be insufficient to prevent differentiation (Kondrashov, Yampolsky & Shabalina, 1998). These considerations lead to the prediction that ring species can form in the absence of ecological divergence only when effective gene flow between the terminal forms is small. On the other hand, they should readily form when ecological conditions vary around the ring, even with fairly high levels of gene flow through the chain of populations. We examine these predictions with respect to a well-studied ring species (the Greenish warbler) in a later section of the paper.

Review of ring species

Proposed cases of ring species can be evaluated with respect to four questions. First, do two distinctive forms coexist? Second, is there gene flow between the distinctive forms through a chain of populations? Third, does the chain of populations form a true geographic ring or are there gaps? Fourth, are the terminal forms connected by gradual geographical variation? In an ideal ring species, the answer to all these questions would be 'yes'. In his 1963 book, Mayr listed 18 cases of 'circular overlaps' (an additional five were mentioned only in passing and with poor citation so they are not included in our review). We reviewed the literature on the cases listed by Mayr (1963) plus examples mentioned by others as possible ring species (Table 1). Many of the cases have received very little attention from researchers, making it difficult to assess whether they display the characteristics of ideal ring species.

Most of the proposed cases have the first element of an ideal ring species: coexistence in one area of two closely related but distinctive forms. But in many of the cases there is some hybridization between the terminal forms. In the Great Tit *Parus major* and the Crimson and Yellow Rosellas *Platycercus elegans* and *P. flaveolus*, researchers have found hybrid zones between forms that were thought not to hybridize when they were originally described as members of ring species. Rare hybridization also occurs between the terminal forms in both *Ensatina* salamanders and *Larus* gulls, but in these cases the forms differ strikingly in color patterns and have always been considered distinctive species where they meet. One of the proposed cases, the Tsetse-fly *Glossina morsitans*, has no overlap between the terminal forms.

It is difficult to determine in the majority of proposed cases whether gene flow occurs between the terminal forms through the chain of intermediate populations. Researchers have attempted to use molecular variation to determine patterns of gene flow in only six systems (the *Larus* gulls, the Greenish warbler *Phylloscopus trochiloides*, *Ensatina* salamanders, *Perognathus* mice, *Rhymogona* millipedes, and the African acacia *Acacia karroo*). These attempts are complicated by the fact that both historical biogeographic processes and contemporary gene flow affect patterns of molecular variation. For instance, observations of breeding colonies of *Larus* gulls have suggested that at several places around the ring (Figure 3) neighboring taxa appear to be reproductively isolated, hybridizing only rarely. But both allozymes and AFLP markers show little molecular divergence among taxa in the *Larus* ring (Ryttman, Tegelström & Jansson, 1980; Johnson, 1985; Snell, 1991; de Knijff et al., 2001). This could be the result either of high gene flow throughout the ring or a recent range expansion, or both. Thus it is difficult to conclude whether gene flow in this complex is high (as suggested by molecular variation) or low (as suggested by the low frequency of interbreeding between neighboring forms). But *Larus* does demonstrate that significant species-level differentiation can develop with little differentiation in molecular markers. Unlike *Larus*, all of the other cases in which molecular variation has been studied have strong genetic differences between different populations. Such

Table 1. A summary of species complexes that have been described as ‘circular overlaps’ or ‘ring species’. For each case, we describe whether there is sympatry of terminal forms (i.e., separate species), summarize the known differences between the terminal forms, and show whether there is evidence for significant gene flow between those forms through the ring of populations. Few of the cases have the characteristics of ideal ring species, and more research is needed to evaluate many of them.

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
Crested Honey-buzzard (*Pernis ptilorhyncus*) and Barred Honey-buzzard (*P. celebensis*).	Yes	Coloration, morphology habitat (altitude)	Unknown	Two forms coexist in the Philippines and there seem to be intermediate forms on islands to the southwest.	Mayr, 1942, 1963; Thiollay, 1994
Herring Gull (*Larus argentatus*) and Lesser Black-backed Gull (*L. fuscus*)	Yes, with some hybridization	Coloration, morphology	Yes, or recent expansion and divergence (allozymes and AFLP)	A very complex situation, involving many taxa. Two forms coexist in Europe, with a chain of gradating forms around the Arctic Ocean connecting them. There may be several places around the ring where neighboring forms rarely interbreed. Studies of neutral genetic markers have found little difference between taxa, indicating high gene flow or recent expansion and differentiation. See Figure 3.	Mayr, 1942, 1963; Ryttman, Tegelström and Jansson, 1980; Harrison, 1985; Johnson, 1985; Snell, 1991; Burger and Gochfeld, 1996; de Knijff et al., 2001
Ringed Plover (*Charadrius hiaticula*) and Semipalmated Plover (*C. semipalmatus*)	Yes	Vocalizations, coloration, morphology	Unlikely	Bock (1959) thought this might be a circumpolar ring species, with coexistence of the terminal forms on Baffin Island, although mixed pairs have been seen there. It now appears that there are distinctive species on either side of the Bering Strait, and hence that this is not a ring species.	Bock, 1959; Mayr, 1963; Smith, 1969; Hayman, Marchant and Prater, 1986; Wiersma, 1996

Table 1. (*continued*)

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
Crimson Rosella (*Platycercus elegans*), Adelaide Rosella (*P. adelaidae*) and Yellow Rosella (*P. flaveolus*)	Hybrid zone	Coloration, habitat	Yes (hybridization)	Three forms occur in adjacent regions of southeast Australia. Cain (1955) thought there was coexistence between *elegans* and *flaveolus* without hybridization and that *adelaidae* was intermediate. In fact, it appears that all three forms hybridize where they meet.	Cain, 1955; Mayr, 1963; Collar, 1997
Collared Kingfisher (*Todiramphus chloris*) and Micronesian Kingfisher (*T. cinnamominus*)	Yes	Coloration	Unlikely	*T. chloris* is one of the most variable of all bird species, with 49 geographic races. *T. cinnamomina* coexists with *T. chloris* on Palau, but also occurs alone on Guam (now close to extinction) and Caroline Islands. If not for coexistence of different forms Palau, the two might be considered a single species. A similar situation occurs in the Talaud Islands, where *T. enigma* occurs alongside *T. chloris* without interbreeding.	Mayr, 1942, 1963; Pratt, Bruner and Berrett, 1987; Fry and Fry, 1992; Woodall, 2001

Table 1. (*continued*)

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
Eurasian Skylark (*Alauda arvensis*), Japanese Skylark (*A. japonica*) and Oriental Skylark (*A. gulgula*)	Yes	Morphology vocalizations	Unlikely	In central Asia, a northern form, *arvensis*, and a southern form, *gulgula*, coexist without interbreeding. These forms are separated by a gap in distribution in northern China, but a morphologically intermediate form, *japonica*, occurs in Japan. Northern *japonica* are similar to *arvensis* and southern *japonica* resemble *gulgula*.	Vaurie, 1951; Mayr, 1963; MacKinnon and Phillips, 2000
Greenish Warbler (*Phylloscopus trochiloides*)	Yes	Vocalizations, coloration, migration routes	Limited (microsatellites, mtDNA)	An almost continuous chain of intergrading forms around the Tibetan Plateau, with two distinctive forms in sympatry in Central Siberia. See text and Figures 5 & 6 for more details.	Ticehurst, 1938; Mayr 1942, 1963; Williamson, 1962; Martens, 1980; Irwin, 2000; Irwin, Bensch and Price, 2001
Chiffchaff (*Phylloscopus collybita*) and Mountain Chiffchaff (*P. sindianus*).	Yes	Habitat, vocalizations, coloration (subtle)	Unlikely	The two forms coexist in the mountains of the western Caucusus, but the chain connecting them through possibly intermediate forms in central Asia and western Russia has a major gap and possibly one or two species boundaries.	Ticehurst, 1938; Mayr, 1942, 1963; Martens, 1982; Martens, 1996; Helbig et al., 1996; Baker, 1997

Table 1. (*continued*)

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
Sulawesi Triller (*Lalage leucopygialis*), Pied Triller (*L. nigra*), and White-shouldered Triller (*L. sueurii*)	Yes	Vocalizations, habitat	Unknown	Two forms (*leucopygialis* and *sueurii*) coexist on Sulawesi Island. Each is similar to *nigra*, an intermediate form that occurs on other islands.	Mayr, 1942, 1963; Holmes and Phillipps, 1996
Brown Thornbill (*Acanthiza pusilla*) and Tasmanian Thornbill (*A. ewingii*)	Yes	Vocalizations, habitat coloration (subtle)	Unlikely	Two forms coexist in Tasmania, but each is very similar to Australian *A. pusilla*.	Lack, 1947; Simpson, Day and Trusler, 1999; Blakers, Davies and Reilly, 1984
Great Tit (*Parus major*)	Hybrid zones	Habitat, vocalizations coloration	Limited (hybridization between groups)	Four group of subspecies, in which distributions form two continuous rings in Asia with hybridization where the different groups meet, apparently in secondary contact. In the Amur River region of eastern Russia, two distinctive forms occur and were thought to be the terminal forms of a ring, although it is now known that there is some hybridization there.	Mayr, 1942, 1963; Harrap and Quinn, 1995; Martens, 1996
Large Tree-finch (*Camarhynchus psittacula*) and Medium Tree-finch (*C. pauper*)	Yes	Morphology, food preference	Unknown	Two forms occur on Floreana Island, in the Galapagos, and intermediates occur on nearby islands. See text and Figure 4.	Lack, 1947; Mayr, 1963; Grant, 1986

Table 1. (*continued*)

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
Salamander (*Ensatina eschscholtzii*)	Yes, with some hybridization	Coloration	Limited (allozymes, mtDNA)	Two distinctive forms coexist in the mountains of southern California, while a chain of gradually intermediate forms connects them through a ring of mountains to the north. Genetic markers suggest that gene flow is severely restricted at several points around the ring. See text and Figure 2.	Stebbins, 1949, 1957; Mayr, 1963; Brown, 1974; Wake and Yanev, 1986; Wake, Yanev and Brown, 1986; Moritz, Schneider and Wake, 1992; Jackman and Wake, 1994; Highton, 1998; Wake and Schneider, 1998
Japanese pond frogs (*Rana nigromaculata* and *R. brevipoda*)	Yes, with some hybridization in the distant past	Breeding time and place, morphology	Unlikely	Two distinctive forms occur in Japan, although they appear to have interbred in the past. The mainland Asian form appears to be intermediate. Little information is available.	Moriya, 1960; Mayr, 1963
Deer Mouse (*Peromyscus maniculatus*)	Yes	Habitat, morphology, mate preference	Unknown	Many cases of circular overlaps in this complex group that is distributed throughout North America. In some places two forms come into contact without interbreeding, but in other places there appear to be gradients with gene flow between the forms.	Dice, 1940; Mayr, 1942, 1963; Blair, 1950; Caire and Zimmerman, 1975

Table 1. (*continued*)

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
House Mouse (*Musculus musculus*)	Hybrid zones	Morphology, habitat	Unknown	Three expansions out of northern India now meet in two narrow hybrid zones, in Europe and China. The hybrid zone in Europe shows some genetic dysfunction.	Bonhomme et al., 1994
Pocket Mice (*Perognathus amplus* and *P. longimembris*)	Yes	Morphology	No (mtDNA)	Two similar forms coexist with little interbreeding in the south. In the north, the two species are almost indistinguishable but are separated by the Colorado River, across which there appears to be no gene flow.	Hoffmeister, 1986; McKnight, 1995
Bee (*Hoplitis producta*)	Yes	Morphology	Unlikely	Two forms have been found in southern California, where they apparently behave as separate species. Michener (1947) felt that they are connected through a chain of intermediate subspecies encircling the Great Basin, but there are major gaps in distribution.	Michener, 1947; Mayr, 1963
Butterfly (*Junonia coenia* and *J. genoveva*/*J. evarete*)	Yes	Coloration	Unlikely	Two colonizations of Cuba, one from South America and one from North America. There is clear intergradation from north to south through Mexico.	Mayr, 1942, 1963; Brown and Heineman, 1972; Schwartz, 1989

Table 1. (*continued*)

Proposed cases of ring species	Sympatry of terminal forms?	Known differences between terminal forms	Gene flow around ring?	Notes on distribution and geographic variation	References
Tsetse-flies (*Glossina morsitans*)	No	Morphology of genitalia	Unknown	Laboratory experiments show there is a geographical gradient of forms, the most distant of which are reproductively incompatible. But there is no overlap, and hence this is not a ring species.	Vanderplanck, 1948; Mayr, 1963
Fruit fly (*Drosophila paulistorum*)	Yes	Morphology of genitalia (extremely subtle)	Unknown	Laboratory experiments indicate that a ‘transitional race’ can sometimes interbreed with several other races that are otherwise reproductively isolated from one another. See text and Figure 1.	Mayr, 1963; Dobzhansky and Spassky, 1959; Dobzhansky et al., 1964; Dobzhansky and Pavlovsky, 1967
Millipede (*Rhymogona silvatica* and *R. cervina*)	Hybrid zone	Morphology of genitalia (subtle)	Apparently (allozymes)	Populations appear to have expanded from the north into the Swiss Alps after the last glaciation, and now hybridize where they are in secondary contact.	Scholl and Pedroli-Christen, 1996
African Acacia (*Acacia karroo*)	Introgression	N/A	Yes (allozymes)	This species consists of a geographically variable ring of populations in South Africa, but there appears to be gradual change all the way around the ring, with no place where distinct forms coexist.	Brain, 1989

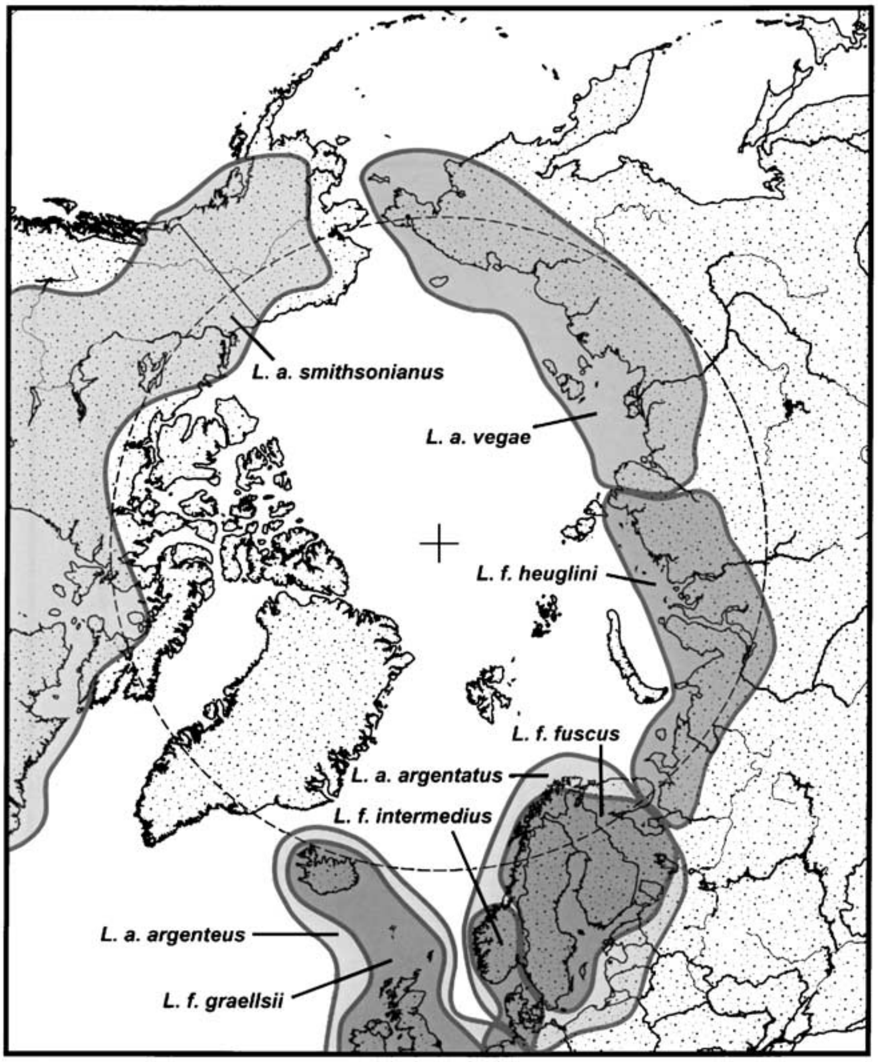

Figure 3. Map of the arctic region showing the circumpolar distribution of subspecies in the Herring Gull/Lesser Black-Backed Gull (*Larus argentatus*/*Larus fuscus*) complex. Subspecies names (following Burger & Gochfeld, 1996) are abbreviated as follows: *L.* = *Larus*; *a.* = *argentatus*; *f.* = *fuscus*. Forms of both *Larus argentatus* and *Larus fuscus* coexist in Europe, where they are highly distinctive. A chain of intermediate forms connects them around the Arctic Ocean. The form *heuglini* is variably considered a subspecies of *L. fuscus* (Burger & Gochfeld, 1996) or of *L. argentatus* (Harrison, 1985). Although hybridization has often been observed between taxa, even between European *fuscus* and *argentatus*, there is also some amount of reproductive isolation between several neighboring taxa around the ring: between *smithsonianus* and *vegae*, between *vegae* and *heuglini*, and between *heuglini* and *fuscus*. Molecular markers show little differentiation between taxa, suggesting recent expansion and differentiation (Johnson, 1985; Snell, 1991; de Knijff et al., 2001).

patterns in neutral markers could result either from current barriers to gene flow, past geographic isolation followed by recent expansion and introgression, or from isolation-by-distance.

However, many proposed ring species lack continuous geographic ranges, making significant ongoing gene flow throughout the chain of intermediate populations unlikely. For example, the butterfly *Junonia lavinia* apparently colonized the island of Cuba from both North and South America, and as a result two forms in Cuba coexist. But dispersal between Cuba and mainland North and South America must be extremely rare, such that current gene flow plays no significant role. In fact, seven of the cases that Mayr (1963) proposed consist of such island invasions. There are many additional examples of double invasions that Mayr did not list (Grant, 1968; Coyne & Price, 2000). Several of the non-island examples, such as *Perognathus* pocket mice and *Charadrius* plovers, now have major geographic barriers to dispersal somewhere in the chain connecting the terminal forms. It is ironic that most suggested cases of 'circular overlap' have no continuous circle of populations.

Hence few of the cases qualify as ideal ring species due to the presence of major gaps in distribution, likely leading to a lack of significant gene flow through the chain of populations. Why, then, did Mayr call them 'the perfect demonstration of speciation'? Mayr (1963) thought that all of the cases he cited had one essential characteristic in common: in each case, two distinct forms coexisted in one place, but forms elsewhere had intermediate characteristics, even when there were breaks in distribution or gene flow (however, the *Charadrius* plovers do not appear to have intermediate forms, and more research is needed to evaluate some of the other cases). For systematists, this creates an apparent paradox; the two sympatric forms can be considered as separate species where they coexist, and yet they can also be considered the same species because of the chain of intermediate forms. For example, the Large Tree-finch *Camarhynchus psittacula* and Medium Tree-finch *C. pauper* both occur on Floreana Island without interbreeding, but are connected through a series of intermediate forms on nearby islands (Figure 4; Lack, 1947; Grant, 1986). Lack (1947) felt that if *C. psittacula* did not occur on Floreana, *C. pauper* would be considered a subspecies of *C. psittacula*. The progressive differences in the morphology of these finches through the chain of islands, with the most divergent forms coexisting and reproductively isolated on the same island, provides a demonstration of how small changes can eventually become species-level differences. It is this link between microevolution and speciation that Mayr (1942, 1963) was emphasizing when he described such cases as circular overlaps. The link is especially clear in two cases that have been well-studied, the *Ensatina* salamanders (Stebbins, 1949; Brown, 1974; Wake & Yanev, 1986; Wake, Yanev & Brown, 1986; Moritz, Schneider & Wake, 1992; Jackman & Wake, 1994; Wake & Schneider, 1998) and the Greenish warbler, which we review below.

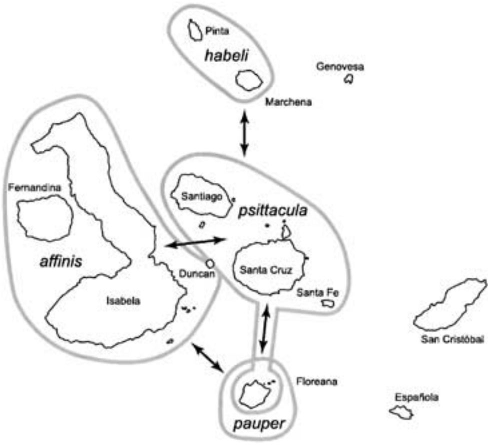

Figure 4. Distributions of various forms of the Large Tree finch *Camarhynchus psittacula* and Medium Tree finch *C. pauper* in the Galápagos islands, redrawn from Lack (1947). The two forms coexist on Floreana Island, but through the other islands there is a chain (represented by arrows) of progressively intermediate forms: *C. pauper* on Floreana – *C. psittacula affinis* on Isabela – *C. psittacula affinis*/*C. psittacula psittacula* intermediates on Duncan – C. *psittacula psittacula* on Santa Cruz – *C. psittacula psittacula* on Floreana. *C. p. habeli* on Pinta and Marchena is a member of the complex, but not part of the ring.

The Greenish warbler complex

The Greenish warbler, *Phylloscopus trochiloides*, is a small (∼7g.) insectivorous leaf-gleaning bird that breeds in forests over a range spanning much of the Palaearctic (Figure 5(a)). Based on variation in museum specimens, Ticehurst (1938) described the Greenish warbler complex as consisting of six subspecies, five of which form a ring around the Tibetan Plateau. Ticehurst (1938) felt that two of the subspecies coexisted without interbreeding in the Yenisey River valley of central Siberia, with gradual variation through the chain of populations to the south. The main morphological characteristic that differs between the west Siberian form, *viridanus*, and the east Siberian form, *plumbeitarsus*, is the size of pale stripes on the birds' wings; these wing bars are small in *viridanus*, large in *plumbeitarsus*, and gradually vary around the southern side of the ring. Both Ticehurst (1938) and Mayr (1942) felt that the Greenish warbler was a ring species that formed when an ancestral species in the Himalayas expanded northward along two pathways on either side of the Tibetan Plateau. We have studied this proposed ring species using molecular techniques, playback experiments, and song spectrogram analysis in addition to analyses of morphological variation.

We reconstructed the history of the Greenish warbler complex using mitochondrial DNA sequences and two microsatellite loci (Irwin, Bensch & Price, 2001). A simplified mtDNA gene tree is shown in Figure 5(b). The gene tree has a great deal of geographic structure, with two major clades correspond-

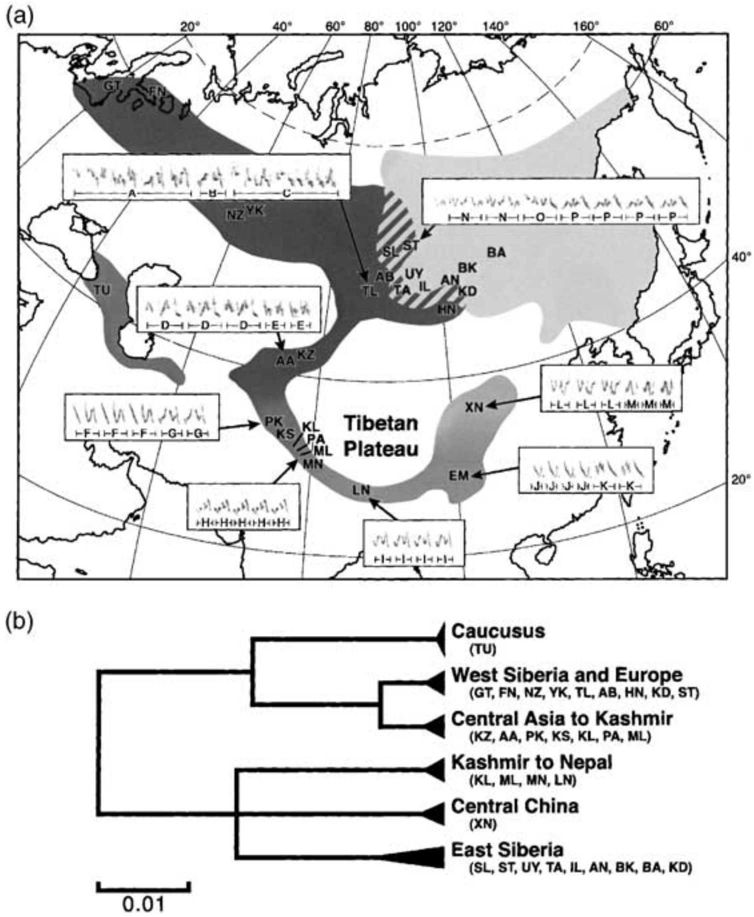

Figure 5. The Greenish warbler (*Phylloscopus trochiloides*) species complex. (a) Map of Asia showing the breeding range. The shading represents gradual geographical variation around the western, southern, and eastern sides of the Tibetan Plateau (Ticehurst, 1938; Irwin, Bensch & Price, 2001). In central Siberia, the west Siberian form *viridanus* (dark gray) and the east Siberian form *plumbeitarsus* (light gray) coexist without interbreeding. Also shown are the locations of research sites (indicated by their two-letter designations) and representative song spectrograms from eight locations around the ring (Irwin, 2000). Songs are long and complex in the north, but the two Siberian forms distinctly differ in song structure. There is a gradient in songs around the ring, with short and simple songs in the south. (b) A simplified mitochondrial gene tree showing phylogeographic relationships among populations, based on sequences of 1200 b.p. of DNA from 149 individuals (modified from Irwin, Bensch & Price, 2001). The letters in parentheses at the tip clades indicate the research sites from which members of each tip clade were sampled, and the length of the black triangle at each tip represents the amount of variation in that clade. The scale bar represents the substitution rate along a lineage.

ing to western and eastern Greenish warblers. In central Siberia, each individual's song type (*viridanus* or *plumbeitarsus*) always corresponded to its mitochondrial haplotype ($n = 17$ *viridanus* and 35 *plumbeitarsus*). This indicates that the Siberian forms had separate origins and are reproductively isolated. The two clades also come into contact in a 200 km wide region of the western Himalayas, where individuals of the two clades do not differ in plumage, morphology or songs, and apparently interbreed. Both microsatellite loci also show strong differences between the Siberian taxa, little south to north variation, and steep change through the western Himalayas (Irwin, Bensch & Price, 2001).

Overall, the variation is in accord with a recent spread north along two pathways, as may be expected given the inhospitable climate in Siberia during Pleistocene glaciations. Based on mitochondrial cytochrome *b* sequences (Price, Helbig & Richman, 1997) and a clock calibration of cytochrome *b* divergence at the rate of 2% per million years (Klicka & Zink, 1997), the deepest split in the mitochondrial gene tree occurred 2–3 million years ago. This suggests the complex has had a long history in the southern part of its present range. It is possible that the phylogeographic structure developed in a continuous isolation-by-distance model in the absence of any geographic break (D. Irwin, unpublished). However, the alternative, that there was geographical separation of the western and eastern parts of the complex and relatively recent contact between them, cannot presently be rejected. Currently populations do seem to be connected, and there is continuous variation in morphology, song structures, and plumage patterns throughout the ring (Irwin, Bensch & Price, 2001). The only major gap in distribution, in northern China, is attributable to recent forest destruction by humans, and the forms on either side of the gap are very similar.

Given the inferred history of this ring species, we can reconstruct the evolution of traits associated with reproductive isolation. These include plumage patterns such as the wing bar, discussed above, and song. Within birds, male song is used in mate attraction, territory defense and species recognition (Catchpole & Slater, 1995), especially within *Phylloscopus* warblers (Martens, 1980; Salomon, 1989). We have analyzed songs recorded throughout the range of the Greenish warbler, and have found pronounced geographic variation (Figures 5(a), 6; Irwin, 2000). Greenish warblers exhibit tremendous variety in the songs that they sing, but all songs are constructed out of a limited number of distinct 'song units' (Irwin, 2000). The apparently ancestral Himalayan form sings short and simple songs consisting of a single song unit repeated four to six times. The two Siberian forms distinctly differ in the songs that they sing, but elsewhere around the ring songs change gradually. The west Siberian form, *viridanus*, sings long, complex songs made of long song units with a large frequency range. The east Siberian form, *plumbeitarsus*, also sings long, complex songs, but they are made of many shorter song units with a smaller frequency range. Playback experiments have shown that males of the two Siberian forms do not recognize each other's songs (Irwin, Bensch & Price, 2001). Although we have not directly studied female choice, theory and research on other bird species indicate that females are generally more discriminating on song when choosing mates than males are when recognizing competitors (Searcy & Brenowitz, 1988). During the northward expansions, songs appear to have evolved in parallel in terms of length and complexity, while diverging in unit length and song structure (Figure 6). The increasing song complexity northward on both sides of the ring could be the result of increased sexual selection or reduced costs of singing in the north (Irwin, 2000). Other aspects of singing behavior, such as the percent of time spent singing and the repertoire length of individual birds, differ between northern and southern populations in a way that suggests that songs are more important at higher latitudes (Irwin, 2000).

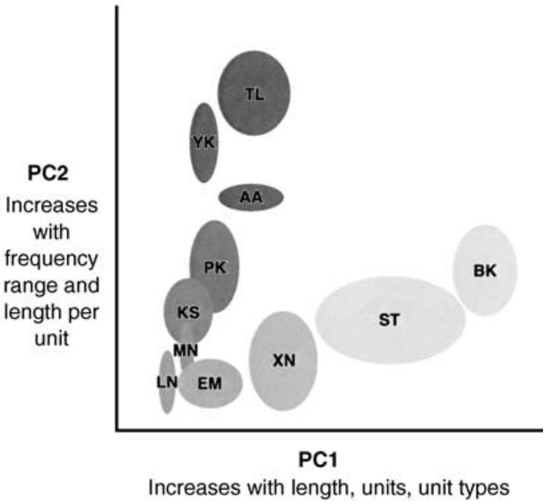

Figure 6. Geographic variation in songs of Greenish warblers, quantified by principle components analysis. Population means are indicated by the two-letter designations for the research sites in Figure 5(a), and standard deviations are indicated by the sizes of the gray ellipses. The shade of gray represents the location of each population in Figure 5(a). Songs distinctly differ between west Siberian *viridanus* (dark gray) and east Siberian *plumbeitarsus* (light gray), but change gradually through the chain of populations to the south. Both PC1 and PC2 are axes of complexity, but they are independent forms of complexity. Himalayan populations have the simplest songs (e.g., sites LN, MN), and songs increase in complexity to the north, both to the west of the Tibetan plateau (increase along PC2) and to the east (increase along PC1).

These inferences illustrate the value of ring species. Without the chain of populations connecting the two reproductively isolated forms we would have little understanding of how song differences had been generated. Using any form of ancestral reconstruction (e.g., parsimony) we would have concluded that the ancestral songs of the two Siberian forms were long and complex, because both forms share these features. In fact, the evolution of complex songs from simple ones has probably been critical in their divergence around each side of the ring. There are many ways to be complex, and small differences among simple songs (in the west and east of the Himalayas) may have been amplified into highly distinctive complex songs. Hence the fact that the Greenish warbler is a ring species is useful in two ways. First, the clear gradient in song characteristics around the ring shows that small changes in song can accumulate into species-level differences. Second, the variation gives us essential insights into what is causing speciation. We can use these insights to evaluate alternative ecological and geographical models of species' differentiation.

Geographical versus ecological divergence

In a model of ecological differentiation, divergent selection pressures in different environments result in speciation. However, in the case of the Greenish warbler, the two reproductively isolated forms in Siberia appear to be more similar ecologically than each is to their Himalayan ancestor. Greenish warblers in the Himalayas inhabit sparsely wooded areas near treeline, whereas populations in both western and eastern Siberia inhabit dense lowland forest consisting of a mixture of broad-leaved and coniferous trees. Populations at intermediate latitudes inhabit forests with intermediate characteristics. Northern populations also differ from southern ones in such factors as population density, food abundance, day length, and length of breeding season, and each of these factors differs relatively little between western and eastern populations at the same latitude (Irwin, 2000). Thus it appears that ecological selection pressures have changed in parallel during both northward expansions. This pattern is reflected in variation in body size; *viridanus* and *plumbeitarsus* are each about 10% smaller than Himalayan birds. Rather than being a product of divergent ecological selection, the two reproductively isolated forms appear to have undergone parallel ecological evolution. Their ecological similarity may account for the failure of either to penetrate far into each other's range (Figure 5(a); Irwin, Bensch & Price, 2001).

One ecological trait that has diverged between the western and eastern forms is their migratory behavior (Ticehurst, 1938; Williamson, 1962). The western forms winter in India, and the eastern forms in southeast Asia (Williamson, 1962). It is possible that hybrids take an intermediate migratory direction (e.g., into Tibet) and therefore have reduced fitness (see Helbig (1991) for a demonstration of a similar phenomenon in a European warbler). Thus there may be some degree of ecologically imposed post-mating isolation, but this remains undetermined. However, the fact that major aspects of singing behavior (e.g., increased song length, complexity, time spent singing, and repertoire length) have evolved in parallel suggests that songs of west and east Siberian forms have responded to similar selection pressures. We attribute the divergence in songs to the amplification of small differences in the southern part of the range, during selection for increased length and complexity. In this way pre-mating isolation can evolve in response to parallel rather than divergent selection pressures.

The fact that songs have diverged so significantly during parallel shifts in ecology might suggest that the Greenish warbler is not an example of ecological speciation. On the other hand, under a model of 'pure' geographical speciation the apparently arbitrary differences in song between *viridanus* and *plumbeitarsus* should not have arisen in the absence of a prolonged geographical barrier. But an examination of the Greenish warbler complex leads to the conclusion that such differences can arise, even if gene flow is ongoing. Assuming that the difference in song complexity between southern and northern populations is adaptive, song variants are unlikely to spread from one of the Siberian forms south through the Himalayan forms and into the other Siberian form. This is not because of a lack of gene flow around the ring, but rather because those song features that are associated with increased complexity (unit length in the west, unit number in the east) are at a selective disadvantage in the south. In terms of the adaptive surface model of evolution (Fear & Price, 1998), for the Siberian forms the two kinds of songs in the north represent adaptive peaks of similar height, and the shorter songs in the south an adaptive valley separating these peaks. Because of geography and the reproductive isolation in central Siberia, evolution of the western song into the eastern song has to be through such a fitness valley.

Our analysis suggests that neither an ecological nor a geographical model of speciation as they are commonly described applies to the Greenish warbler complex. Instead, it appears that parallel ecological changes have led to the kind of divergence in sexually selected traits that normally occurs only between completely allopatric populations. These kinds of interactions between ecological selection pressures and sexual selection may be a more common way of producing diversity than is currently appreciated.

Conclusion

Mayr (1970, p. 320) viewed ring species as demonstrations of 'orthodox geographic speciation', or speciation as a result of the complete cessation of gene flow between two groups. However, as discussed above, theoretical considerations lead to the prediction that ring species can form even with gene flow around the ring, especially when there are ecological differences among populations. Many of the proposed cases in Table 1 have terminal forms that differ in habitat preference and/or morphology, suggesting that ecological divergence has played a role. However, in most of the cases the relative importance of divergent selection or arbitrary changes due to genetic isolation has not been determined. Even when there are no ecological differences between the terminal forms, our analysis of the Greenish warbler suggests that differences can arise if the two terminal forms have undergone parallel shifts in ecological conditions. Further study of proposed cases of ring species will lead to a better understanding of how ecological divergence and geographic separation interact to cause speciation.

Since we can learn so much about speciation from ring species, it would be helpful if there were more known cases. Given that we have only found 23 proposed examples, they appear to be quite rare. However, this could be a result of scientific methodology. There have been few attempts to compile lists of ring species, and most proposed examples are from well-studied taxa such as birds. Furthermore, taxonomic methodology creates a bias against finding ring species. Traditional taxonomy operates by classifying organisms into specific groups (e.g., species) that are organized into hierarchies (e.g., genera, families, etc.). Ring species simply cannot fit into such a classification structure since they consist of a spectrum of forms rather than well-defined groups. When ring species are forced into the traditional taxonomic structure they are either lumped together as a single species or arbitrarily split into two or more species. Both treatments obscure the existence of a gradient of forms between two species. The ring of Greenish warbler populations, for instance, is generally treated by taxonomists as either a single species (e.g., Vaurie, 1959; Dementev & Gladkov, 1968; Monroe & Sibley, 1993; Beaman, 1994) or as the two species *Phylloscopus plumbeitarsus* (consisting of just the east Siberian subspecies) and *P. trochiloides* (consisting of the other subspecies around the ring) (e.g., Williamson, 1962; Martens, 1980; Sibley & Monroe, 1990; Cramp, 1992). In the latter treatment, a species boundary is placed in the distributional gap in northern China, even though birds on either side of the gap are quite similar to each other given the amount of variation in the entire complex (Irwin, Bensch & Price, 2001). Neither taxonomic treatment captures the true relationships within the complex, but the traditional rules of taxonomy allow no other options.

The formation of ring species requires unusual geographic circumstances. Ideal ring species require an almost continuous ring of suitable habitat around a geographic barrier. The scale of the ring clearly needs to be large compared to the distances traveled by individuals of the species. Finally, an ancestral species must undergo range expansion from one side of the barrier to the other along two pathways, and the expansion must occur slowly enough that significant differentiation between the two paths can occur before the differentiating forms meet on the other side of the barrier.

While these conditions are necessary for ideal ring species to form, the continued persistence of a ring species requires stability of habitat around the entire ring. Such stability is unusual over the large areas that are required for ring species to form. Climatic fluctuations can dramatically change habitats, and local extinctions or reductions in the range of any species often occur. Such extinctions, when they occur in ring species, can obscure the history of divergence and create breaks. Ongoing habitat destruction due to human activity is causing ring species to become more difficult to find and study. As a result, our ability to reconstruct the history of speciation using ring species is being rapidly compromised.

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References

Arnqvist, G., M. Edvardsson, U. Friberg & T. Nilsson, 2000. Sexual conflict promotes speciation in insects. Proc. Natl. Acad. Sci. USA 97: 10460–10464.

Baker, K., 1997. Warblers of Europe, Asia, and North Africa. Princeton University Press, Princeton, New Jersey.

Barton, N.H., 1979. Gene flow past a cline. Heredity 43: 333–339.

Beaman, M., 1994. Palearctic Birds: a Checklist of the Birds of Europe, North Africa and Asia North of the Foothills of the Himalayas. Harrier Publications, Stonyhurst, England.

Blair, W.F., 1950. Ecological factors in speciation of *Peromyscus*. Evolution 4: 253–275.

Blakers, M., S.J.J.F. Davies & P.N. Reilly, 1984. The Atlas of Australian Birds. Melbourne University Press, Melbourne.

Bock, W.J., 1959. The status of the Semipalmated Plover. Auk 76: 98–100.

Bonhomme, F., R. Anand, D. Darviche, W. Din & P. Bousot, 1994. The House Mouse as a ring species?, pp. 13–23 in Genetics in Wild Mice: Its Application to Biomedical Research, edited by K. Moriwaki, T. Shiroishi & H. Yonekawa. Japan Scientific Societies Press, Tokyo.

Brain, P., 1989. Genetic races in a ring species, *Acacia karroo*. S-Afr. Tydskr. Wet. 85: 181–185.

Brown, C.W., 1974. Hybridization Among the Subspecies of the Plethodontid Salamander *Ensatina eschscholtzii*. University of California Press, Berkeley.

Brown, F.M. & B. Heineman, 1972. Jamaica and its Butterflies. E.W. Classey Ltd., London.

Burger, J. & M. Gochfeld, 1996. Family Laridae (gulls), pp. 572–623 in Handbook of the Birds of the World, Vol. 3, Hoatzin to Auks, edited by J. del Hoyo, A. Elliott & J. Sargatal. Lynx Edicions, Barcelona.

Cain, A.J., 1954. Animal Species and their Evolution. Hutchinson House, London.

Cain, A.J., 1955. A revision of *Trichoglossus haematodus* and of the Australian platycercine parrots. Ibis 97: 432–479.

Caire, W. & E.G. Zimmerman, 1975. Chromosomal and morphological variation and circular overlap in the deer mouse, *Peromyscus maniculatus*, in Texas and Oklahoma. Syst. Zool. 24: 89–95.

Catchpole, C.K. & P.J.B. Slater, 1995. Bird Song: Biological Themes and Variations. Cambridge University Press, Cambridge.

Collar, N.J., 1997. Family Psittacidae (parrots), pp. 280–479 in Handbook of the Birds of the World, Vol. 4, Sandgrouse to Cuckoos, edited by J. del Hoyo, A. Elliott & J. Sargatal. Lynx Edicions, Barcelona.

Coyne, J. & T. Price, 2000. Little evidence for sympatric speciation in island birds. Evolution 54: 2166–2171.

Cramp, S. (ed.), 1992. Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic. Oxford University Press, Oxford.

Danley, P.D., J.A. Markert, M.E. Arnegard & T.D. Kocher, 2000. Divergence with gene flow in the rock-dwelling cichlids of Lake Malawi. Evolution 54: 1725–1737.

Darwin, C., 1859. The Origin of Species by Means of Natural Selection. John Murray, London.

Dementev, G.P. & N.A. Gladkov (eds), 1968. Birds of the Soviet Union, Vol. 6, Israel Program for Scientific Translations, Jerusalem.

Dice, L.R., 1940. The relation of genetics to geographical distribution and speciation; speciation. II. speciation in *Peromyscus*. Am. Nat. 74: 289–298.

Dieckmann, U. & M. Doebeli, 1999. On the origin of species by sympatric speciation. Nature 400: 354–357.

Dobzhansky, T., 1958. Species after Darwin, pp. 19–55 in A Century of Darwin, edited by S.A. Barnett. Heinemann, London.

Dobzhansky, T. & O. Pavlovsky, 1967. Experiments on the incipient species of the *Drosophila paulistorum* complex. Genetics 55: 141–156.

Dobzhansky, T. & B. Spassky, 1959. *Drosophila paulistorum*, a cluster of species *in statu nascendi*. Proc. Natl. Acad. Sci. USA 45: 419–428.

Dobzhansky, T., L. Ehrman, O. Pavlovsky & B. Spassky, 1964. The superspecies *Drosophila paulistorum*. Proc. Natl. Acad. Sci. USA 51: 3–9.

Ehrlich, P.R. & P.H. Raven, 1969. Differentiation of populations. Science 165: 1228–1232.

Endler, J.A., 1977. Geographic Variation, Speciation, and Clines. Princeton University Press, Princeton, New Jersey.

Endler, J.A., 1992. Signals, signal conditions, and the direction of evolution. Am. Nat. 139: s125–s153.

Fear, K. & T. Price, 1998. The adaptive surface in ecology. Oikos 82: 440–448.

Filchak, K.E., J.B. Roethele & J.L. Feder, 2000. Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. Nature 407: 739–742.

Fry, C.H. & K. Fry, 1992. Kingfishers, Bee-Eaters and Rollers. Princeton University Press, Princeton, New Jersey.

Futuyma, D.J. & G. Mayer, 1980. Non-allopatric speciation in animals. Syst. Zool. 29: 254–271.

Gavrilets, S., 2000. Waiting time to parapatric speciation. Proc. R. Soc. Lond. B 267: 2483–2492.

Gavrilets, S., H. Li & M.D. Vose, 1998. Rapid parapatric speciation on holey adaptive landscapes. Proc. R. Soc. Lond. B 265: 1483–1489.

Grant, P.R., 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Syst. Zool. 17: 319–333.

Grant, P.R., 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton, New Jersey.

Gulick, J.T.,1890a. Indiscriminate separation under the same environment, a cause of divergence. Nature 42: 369–370.

Gulick, J.T.,1890b. Unstable adjustments as affected by isolation. Nature 42: 28–29.

Gulick, J.T., 1905. Evolution, Racial and Habitudinal. Carnegie Institution of Washington, Washington, D.C.

Harrap, S. & D. Quinn, 1995. Chickadees, Tits, Nuthatches & Treecreepers. Princeton University Press, Princeton, New Jersey.

Harrison, P., 1985. Seabirds: An Identification Guide. Houghton Mifflin, Boston, revised edn.

Hayman, P., J. Marchant & T. Prater, 1986. Shorebirds: An Identification Guide to the Waders of the World. Houghton Mifflin, Boston.

Helbig, A.J., 1991. Inheritance of migratory direction in a bird species: a cross-breeding experiment with southeast-migrating and southwest-migrating blackcaps (Sylvia atricapilla). Behav. Ecol. Sociobiol. 28(1): 9–12.

Helbig, A.J., J. Martens, I. Seibold, F. Henning, B. Schottler & M. Wink, 1996. Phylogeny and species limits in the Palearctic chiffchaff *Phylloscopus collybita* complex: mitochondrial genetic differentiation and bioacoustic evidence. Ibis 138: 650–666.

Highton, R., 1998. Is *Ensatina eschscholtzii* a ring-species? Herpetologica 54: 254–278.

Hoffmeister, D.F., 1986. Mammals of Arizona. University of Arizona Press and Arizona Game and Fish Department, Tuscon.

Holmes, D. & K. Phillipps, 1996. The Birds of Sulawesi. Oxford University Press, Oxford.

Irwin, D.E., 2000. Song variation in an avian ring species. Evolution 54: 998–1010.

Irwin, D.E., S. Bensch & T.D. Price, 2001. Speciation in a ring. Nature 409: 333–337.

Jackman, T.R. & D.B. Wake, 1994. Evolutionary and historical analysis of protein variation in the blotched forms of salamanders of the *Ensatina* complex (Amphibia: Plethodontidae). Evolution 48: 876–897.

Johannesson, K., 2001. Parallel speciation: a key to sympatric divergence. Trends Ecol. Evol. 16: 148–153.

Johnson, C., 1985. Biochemical genetic variation in populations of *Larus argentatus* and *Larus fuscus* in northwestern Europe. Biol. J. Linn. Soc. 24: 349–363.

Jordan, D.S., 1905. The origin of species through isolation. Science 22: 545–562.

Klicka, J. & R.M. Zink, 1997. The importance of recent ice ages in speciation: a failed paradigm. Science 277: 1666–1669.

de Knijff, P., F. Denkers, N.D. van Swelm & M. Kuiper, 2001. Genetic affinities within the Herring Gull *Larus argentatus* assemblage revealed by AFLP genotyping. J. Mol. Evol. 52: 85–93.

Kondrashov, A., L. Yampolsky & S. Shabalina, 1998. On the sympatric origin of species by means of natural selection, pp. 90–98 in Endless Forms: Species and Speciation edited by D.J. Howard and S.H. Berlocher. Oxford University Press, Oxford.

Kondrashov, A.S. & F.A. Kondrashov, 1999. Interactions among quantitative traits in the course of sympatric speciation. Nature 400: 351–354.

Lack, D., 1947. Darwin's Finches. Cambridge University Press, Cambridge.

Lande, R., 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. USA 78: 3721–3725.

MacKinnon, J. & K. Phillips, 2000. A Field Guide to the Birds of China. Oxford University Press, Oxford.

Martens, J., 1980. Lautäußerungen, verwandtschaftliche Beziehungen und Verbreitungsgeschichte asiatischer Laubsänger (*Phylloscopus*). Advances in Ethology. No. 22. Verlag Paul Parey, Berlin.

Martens, J., 1982. Ringförmige Arealüberschneidung und Artbildung beim Zilpzalp, *Phylloscopus collybita*: Das *lorenzii*-Problem. Z. zool. Syst. Evolutionsforsch. 20: 82–100.

Martens, J., 1996. Vocalizations and speciation of Palearctic birds, pp. 221–240 in Ecology and Evolution of Acoustic Communication in Birds, edited by D.E. Kroodsma & E.H. Miller. Cornell University Press, Ithaca, New York.

Mayr, E., 1942. Systematics and the Origin of Species. Dover Publications, New York.

Mayr, E., 1963. Animal Species and Evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

Mayr, E., 1970. Populations, Species and Evolution: An Abridgment of Animal Species and Evolution. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

McKnight, M.L., 1995. Mitochondrial DNA phylogeography of *Perognathus amplus* and *Perognathus longimembris* (Rodentia: Heteromydae): a possible mammalian ring species. Evolution 49: 816–826.

Michener, C.D., 1947. A revision of the American species of *Hoplitis* (Hymenoptera, Megachilidae). Bull. Am. Mus. Nat. Hist. 89: 257–318.

Monroe, B.L., Jr. & C.G. Sibley, 1993. A World Checklist of Birds. Yale University Press, New Haven, Connecticut.

Moritz, C., C.J. Schneider & D.B. Wake, 1992. Evolutionary relationships within the *Ensatina eschscholtzii* complex confirm the ring species interpretation. Syst. Biol. 41: 273–291.

Moriya, K., 1960. Studies on the five races of the Japanese pond frog, *Rana nigromaculata* Hallowell. III. sterility in interracial hybrids. J. Sci. Hiroshima University (B)18: 125–156.

Muller, H., 1942. Isolating mechanisms, evolution and temperature. Biol. Symp. 6: 71–125.

Orr, H.A., 1995. The population genetics of speciation: the evolution of hybrid incompatiblilities. Genetics 139(4): 1805–1813.

Parsons, T.J., S.L. Olson & M.J. Braun, 1993. Unidirectional spread of secondary sexual plumage traits across an avian hybrid zone. Science 260: 1643–1646.

Pratt, H.D., P.L. Bruner & D.G. Berrett, 1987. A Field Guide to the Birds of Hawaii and the Tropical Pacific. Princeton University Press, Princeton, New Jersey.

Price, T., A. Helbig & A. Richman, 1997. Evolution of breeding distributions in the Old World Leaf Warblers (genus *Phylloscopus*). Evolution 51: 552–561.

Rice, W.R. & E.E. Hostert, 1993. Laboratory experiments on speciation: what have we learned in 40 years? Evolution 47: 1637–1653.

Rice, W.R., 1998. Intergenomic conflict, interlocus anatagonistic coevolution, and the evolution of reproductive isolation, pp. 261–270 in Endless Forms: Species and Speciation, edited by D.J. Howard & S.H. Berlocher. Oxford University Press, Oxford.

Rice, W.R., 2000. Dangerous liaisons. Proc. Natl. Acad. Sci. USA 97: 12953–12955.

Ryttman, H., H. Tegelström & H. Jansson, 1980. Isozyme differences in three related Larus species (Aves). Hereditas 92: 117–122.

Salomon, M., 1989. Song as a possible reproductive isolating mechanism between two parapatric forms. The case of the Chiffchaffs *Phylloscopus c. collybita* and *P. c. brehmii* in the Western Pyrenees. Behaviour 111: 270–290.

Schliewen, U.K., D. Tautz & S. Pääbo, 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. Nature 368: 629–632.

Schluter, D. & T. Price, 1993. Honesty, perception and population divergence in sexually selected traits. Proc. R. Soc. Lond. B 253: 117–122.

Scholl, A. & A. Pedroli-Christen, 1996. The taxa of *Rhymogona* (Diplopoda: Craspedosomatidae): a ring species. Part one: genetic analysis of population structure, in Acta Myriapodologica, edited by J.-J. Geoffroy, J.-P. Mauriès & M. Nguyen Duy -Jacquemin. Mém. Mus. natn. Hist. nat. 169: 45–51.

Schneider, C.J., T.B. Smith, B. Larison & C. Moritz, 1999. A test of alternative models of diversification in tropical rainforests: Ecological gradients versus rainforest refugia. Proc. Natl. Acad. Sci. USA 96: 13869–13873.

Schwartz, A., 1989. The Butterflies of Hispaniola. University of Florida Press, Gainesville, Florida.

Searcy, W.A. & E.A. Brenowitz, 1988. Sexual differences in species recognition of avian song. Nature 332: 152–154.

Sibley, C.G. & B.L. Monroe, Jr., 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut.

Simpson, K., N. Day & P. Trusler, 1999. Birds of Australia. Sixth edition. Princeton University Press, Princeton, New Jersey.

Slatkin, M., 1987. Gene flow and the geographic structure of natural populations. Science 236: 787–792.

Smith, H.G., 1969. Polymorphism in Ringed Plovers. Ibis 111: 177–188.

Smith, T.B., C.J. Schneider & K. Holder, 2001. Refugial isolation versus divergent selection: testing alternative mechanisms of evolutionary divergence in four rainforest vertebrates. Genetica 112–113: 383–398.

Smith, T.B., R.K. Wayne, D. Girman & M. Bruford, 1997. A role for ecotones in generating rainforest biodiversity. Science 276: 1855–1857.

Snell, R.R., 1991. Interspecific allozyme differentiation among North Atlantic white-headed Larid gulls. Auk 108: 319–328.

Stebbins, R.C., 1949. Speciation in salamanders of the Plethodontid genus *Ensatina*. Univ. Calif. Publ. Zool. 48: 377–526.

Stebbins, R.C., 1957. Intraspecific sympatry in the lungless salamander *Ensatina eschscholtzii*. Evolution 11: 265–270.

Thiollay, J.M., 1994. Family Accipitridae (hawks and eagles), pp. 52–205 in Handbook of the Birds of the World, Vol. 2, New World Vultures to Guineafowl, edited by J. del Hoyo, A. Elliott & J. Sargatal. Lynx Edicions, Barcelona.

Ticehurst, C.B., 1938. A Systematic Review of the Genus *Phylloscopus*. Trustees of the British Museum, London.

Vanderplanck, F.L., 1948. Experiments in cross-breeding tsetse-flies (*Glossina* species). Ann. Trop. Med. Parasit., Liverpool 42: 131–152.

Vaurie, C., 1951. A study of Asiatic larks. Bull. Am. Mus. Nat. Hist. 97: 431–526.

Vaurie, C. 1959. The Birds of the Palearctic Fauna: A Systematic Reference, Order Passeriformes. H.F. & G. Witherby, London.

Wake, D.B. & C.J. Schneider, 1998. Taxonomy of the plethodontid salamander genus *Ensatina*. Herpetologica 54: 279–298.

Wake, D.B. & K.P. Yanev, 1986. Geographic variation in allozymes in a 'ring species', the plethodontid salamander *Ensatina eschscholtzii* of western North America. Evolution 40: 702–715.

Wake, D.B., K.P. Yanev & C.W. Brown, 1986. Intraspecific sympatry in a 'ring species', the plethodontid salamander *Ensatina eschscholtzii*, in southern California. Evolution 40: 866–868.

Wiersma, P., 1996. Family Charadriidae (plovers): species accounts, pp. 410–442 in Handbook of the Birds of the World, Vol. 3, Hoatzin to Auks, edited by J. del Hoyo, A. Elliott & J. Sargatal. Lynx Edicions, Barcelona.

Williamson, K., 1962. Identification for Ringers. 2. The Genus *Phylloscopus*. British Trust of Ornithology, London.

Wilson, A.B, K. Noack-Kunnmann & A. Meyer, 2000. Incipient speciation in sympatric Nicaraguan crater lake cichlid fishes: sexual selection versus ecological diversification. Proc. R. Soc. Lond. B 267: 2133–2141.

Woodall, P.F., 2001. Family Alcedinidae (kingfishers), pp. 130–249 in Handbook of the Birds of the World, Vol. 6, Mousebirds to Hornbills, edited by J. del Hoyo, A. Elliott & J. Sargatal. Lynx Edicions, Barcelona.