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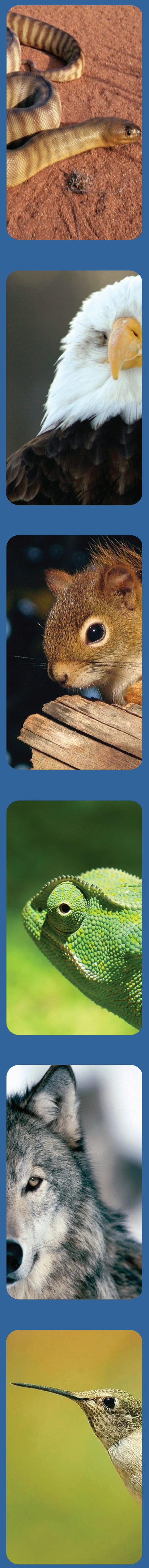
Ignacio Morales Castilla



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Ignacio Morales Castilla

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Tesis Doctoral
Universidad de Alcalá
Departamento de Ecología

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Niche conservatism and evolutionary determinants of terrestrial vertebrate diversity patterns

(Conservación de nicho y determinantes evolutivos de patrones de diversidad de vertebrados terrestres)

Ignacio Morales Castilla

Memoria presentada para optar al grado de Doctor por la Universidad de Alcalá

A thesis supervised by

Miguel Ángel Rodríguez Fernández

Bradford A. Hawkins

Alcalá de Henares, Septiembre de 2011

Universidad
de Alcalá

Departamento de Ecología

Miguel Ángel Rodríguez Fernández, Profesor Titular de Ecología de la Universidad de Alcalá, y como co-director de la Tesis Doctoral,

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado "**Niche conservatism and evolutionary determinants of terrestrial vertébrate diversity patterns**", ha sido realizado bajo su dirección por D. Ignacio Morales Castilla dentro del Programa de Doctorado 'Cambio Global y Desarrollo sostenible', adscrito al Departamento de Ecología de la Universidad de Alcalá. Esta tesis reúne los requisitos propios de este tipo de trabajo: rigor científico, aportaciones novedosas y aplicación de una metodología adecuada. Por lo tanto, doy mi Visto Bueno a la presentación de dicha Tesis Doctoral.

Alcalá de Henares, a 30 de Septiembre de 2011,

Fdo.: Dr. Miguel Ángel Rodríguez Fernández

UNIVERSITY of CALIFORNIA - IRVINE
Ecology & Evolutionary Biology

Bradford A. Hawkins, co-director de la Tesis Doctoral,

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Alcalá de Henares, a 30 de Septiembre de 2011,

Fdo.: Dr. Bradford A. Hawkins

Universidad
de Alcalá

Departamento de Ecología

Julio Camargo Benjumeda, Profesor Titular de Ecología de la Universidad de Alcalá y Director del Departamento de Ecología,

HACE CONSTAR:

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Alcalá de Henares, a 30 de Septiembre de 2011,

Fdo.: Dr. Julio Camargo Benjumeda

A mis padres

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Debían ser las siete de una mañana de invierno de 2001. Fuera comenzaba a amanecer y yo me quedaba dormido con la cabeza apoyada en el cristal del tren. Fue entonces cuando se me ocurrió. Yo quería hacer lo mismo que la persona a cuya clase me disponía a asistir. No sólo eso, yo quería que fuese él quien me guiase en el proceso. Diez años después de aquella mañana parece que me voy acercando a conseguir el primer objetivo. En cuanto al segundo estoy más que satisfecho.

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Trabajar con Brad Hawkins es como contar con un GPS que te marca el camino cuando estás perdido. Tras mirar durante poco más de dos minutos mis primeros resultados, esos que yo había tratado de descifrar durante días, Brad sabía perfectamente lo que significaban… – ¡Está claro!, eso es conservación de nicho – dijo en un correcto castellano. Alguien con una claridad de ideas tan apabullante solo puede despertar admiración. Muchas gracias Brad, por impregnar esta tesis con tu experiencia y sabiduría. Soy muy afortunado por haberte tenido como co-director de la tesis. Gracias por resultar tan inspirador, por enseñarme a entender mis resultados y a poner los pies en la tierra, por tu sentido del humor y por tantos cafés y algunas cervezas hablando de ciencia y de la vida.

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Salir fuera a hacer estancias se hace mucho más llevadero cuando al volver te sientes como en casa y el Departamento de Ecología de la Universidad de Alcalá es una casa llena de caras amigas que hacen el día a día agradable y estimulante. Es un placer haber contado con compañeros y compañeras como Marta (fue genial coincidir en Irvine), Fabio, Mª José, Dani, Luis Cayuela, Oscar, Luis Merino, Kike, Virginia, Bárbara, Itziar, Gonzalo, Lucía, Edu, Pedrarias o Mariano, todos habéis hecho estos años mucho más interesantes y divertidos. Y es un placer hoy día contar con un reemplazo generacional de grandes colegas y amigos como Sara, Noe, Juan, Cristina, Norberto, Belén, Paloma, Silvia, Isa, Guillermo, Carlos, Adolfo y como no Mercedes que me dio la mejor bienvenida a Sydney. Por supuesto el Departamento goza de un óptimo ambiente de trabajo gracias a los y las profesionales que tanto ponen de su parte para que así sea. Pedro, Jose María, Pilar, Julio, Josabel, Asunción, Antonio, Salvador, Josevi, Lorenzo, Ana, Nico, Javi, gracias por hacer marchar la máquina. Una mención especial merece Ana, cuya labor es indispensable para el buen funcionamiento del Departamento. Gracias por tu cercanía, cariño e interés.

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Índice

Resumen

El estudio a gran escala de patrones de diversidad tiene por objeto describir propiedades emergentes de ecosistemas y biotas que en ocasiones no se manifiestan cuando la investigación ecológica se realiza a escalas de detalle. En escalas biogeográficas amplias, los patrones de diversidad son producto de las respuestas de las especies y sus interacciones a las condiciones ambientales actuales y a la variación de las condiciones ambientales en el pasado. Las respuestas a condiciones y cambios ambientales pasados pueden investigarse a partir de fenómenos evolutivos (especiación, extinción) o eventos históricos (dispersión).

El estudio integrado de macroecología y macroevolución es incipiente y la comunidad científica aún se encuentra en fase de desarrollar y consensuar metodologías que permitan dicha integración. Esta tesis utiliza cuatro casos de estudio con el objetivo de avanzar en el conocimiento de los mecanismos que generan los patrones de diversidad integrando aspectos contemporáneos, evolutivos e históricos de las biotas. En el desarrollo de la tesis se han generado bases de datos a partir de datos empíricos de diferentes regiones geográficas, que han sido investigadas utilizando sistemas de información geográfica, modelos estadísticos y técnicas de análisis filogenético. Además, como denominador común se ha empleado el enfoque de ensamblaje, que se caracteriza por usar celdas distribuidas uniformemente a lo largo del territorio como unidad de análisis. La elección de este enfoque responde a que todos los patrones y procesos estudiados se expresan geográficamente y por tanto requieren de aproximaciones espacialmente explicitas para su estudio. Con objeto de conseguir una amplia representatividad, los casos de estudio analizan tres patrones de diversidad (v.g. riqueza de especies, tamaño corporal y tamaño del rango geográfico), tres grupos taxonómicos distintos (v.g. reptiles, aves y mamíferos) y tres regiones de estudio diferentes (v.g. Este y Sur de África, Nuevo Mundo y todo el Globo). Lejos de buscar una

unificación metodológica, los análisis hacen uso de metodologías adaptadas a la idiosincrasia de las preguntas específicas que tratan de responderse en los casos de estudio que se resumen a continuación.

En primer lugar se exploran los patrones de riqueza de especies de cinco grupos de reptiles del Sur y el Este de África y se analizan tanto las relaciones con el clima que observamos en la actualidad, como las probables relaciones ancestrales con los paleoclimas ante los que se originaron esos grupos. Para ello se utiliza la información que proporciona el registro fósil, filogenias datadas y reconstrucciones paleoclimáticas. Encontramos coincidencias entre las condiciones climáticas preferidas en la actualidad y las condiciones climáticas ancestrales para los distintos grupos, lo que sugiere que la conservación de nicho es válida para interpretar los patrones de riqueza de reptiles africanos.

En segundo lugar, se investiga el grado en que las relaciones evolutivas entre especies de aves paseriformes oscines son capaces de explicar sus patrones de tamaño de rango geográfico en el Nuevo Mundo. Los patrones de tamaño de rango se documentan para especies migratorias y no migratorias y se descomponen en la parte que es explicada por las relaciones evolutivas y la que es independiente de dichas relaciones, utilizando análisis filogenéticos de partición de la variación. Los resultados sugieren que el tamaño de rango geográfico es moderadamente heredable para este grupo de aves y por tanto la evolución juega un papel a tener en cuenta en su estudio. Además los patrones encontrados para las aves migratorias y no migratorias difieren entre sí, reflejando las dinámicas migratorias y apoyando en general, el efecto de los gradientes climáticos de mesoescala que se producen en regiones montañosas. Las diferencias regionales y la estructura filogenética encontrada en rangos migratorios, hacen pensar que será conveniente incluir otros rasgos biológicos como la capacidad dispersora, para alcanzar una mejor comprensión de los procesos que condicionan la biogeografía del tamaño de rango de oscines.

En tercer lugar, se examinan las contribuciones de las relaciones evolutivas basales al gradiente global de tamaño corporal de aves, distinguiendo entre la parte del gradiente que está estructurada filogenéticamente y la parte que es independiente de la filogenia y por tanto podría responder a fenómenos adaptativos por debajo del nivel de familia. En este caso se utilizan además de la partición filogenética de la varianza, regresiones parciales para discernir entre las porciones de la variación del tamaño corporal de aves que se explican por la filogenia, por gradientes ambientales o por ambos de forma simultánea. Los resultados muestran una fuerte influencia de las relaciones evolutivas sobre el gradiente de tamaño corporal. Además señalan a la productividad primaria, bien asociada a la temperatura en el Nuevo Mundo o a la estacionalidad en el Viejo Mundo, como mejor descriptor ambiental para el tamaño de aves. Esto apoya a las hipótesis de resistencia a la escasez de recursos y de conservación de calor para explicar la porción del tamaño corporal que es independiente de las relaciones evolutivas.

Finalmente, se inspeccionan los efectos que han podido tener sobre el gradiente de tamaño corporal de mamíferos, eventos históricos de dispersión a gran escala como los intercambios bióticos ocurridos durante el Pleistoceno entre Asia y Norte América o entre las Américas. Asimismo, se comparan los patrones de tamaño corporal de los grupos de mamíferos que participaron en los intercambios bióticos con los que no participaron y se documentan sus señales filogenéticas y sus asociaciones con gradientes ambientales. Los resultados informan de una fuerte influencia de los mamíferos alóctonos sobre el gradiente de tamaño corporal de todas las especies, que además está localizada geográficamente. También se encuentran marcadas diferencias entre los tamaños de los grupos de mamíferos autóctonos y alóctonos en cuanto a sus relaciones con el clima y sus señales filogenéticas. Estas diferencias pueden interpretarse en base a la llegada más reciente de las especies alóctonas a Norteamérica y Sudamérica en combinación con dinámicas de conservación de nicho.

Los resultados de esta tesis son relevantes en el campo de la macroecología y ponen de manifiesto que la inclusión de procesos evolutivos e históricos es clave para entender los patrones biogeográficos de diversidad. Las relaciones filogenéticas, las asociaciones ancestrales con los paleoclimas, el registro fósil o los intercambios bióticos ocurridos debido a cambios paleogeográficos son factores que deben ser tenidos en cuenta para responder preguntas que nos acerquen a conocer mejor el papel de la conservación de nicho en la configuración de la biota de distintas regiones.

Summary

Large scale study of diversity patterns has the purpose of describing emergent properties of the ecosystems and biota which in occasions do not manifest in more detail-scale investigations. At the biogeographic and macroecological scales, diversity patterns are the product of biota's responses to current environmental conditions and past environmental changes that can be researched based on evolutionary phenomena (speciation, extinction) or historical events (dispersion).

Works integrating macroecology and macroevolution are developing and the scientific community is still on the phase of creating and trying to reach a consensus on methodologies allowing such integration. This thesis uses four case studies with the aim of supporting the suitability of schemes incorporating contemporary, evolutionary and historical aspects of the biotas to reach more complete explanations for the mechanisms generating diversity patterns. During the development of this thesis we have created databases using empirical data from different geographical regions, which have been analyzed using geographical information systems, statistical models and phylogenetic analysis methods. Besides, all case studies share in common the assemblage approach, which uses grid cells uniformly distributed across the study area as analysis units. The choice of this approach is related to the fact that all patterns and processes studied have a geographical expression and therefore their study requires spatially explicit methods. Intending to achieve a wide range of representation, the case studies analyze three diversity patterns (i.e. species richness, body size, range size), three different taxonomic groups (i.e. reptiles, birds and mammals) and three geographical regions (i.e. East and South of Africa, the New World, the Globe). Far from trying to find methodological unification, the analyses are adapted to the idiosyncrasy of each specific question that are studied in the following cases.

In the first place, we explore the species richness patterns of five reptile groups from South and East Africa and both relationships with current climate and probable ancestral relationships with palaeoclimates where the groups were originated are analyzed. Information provided by the fossil record, dated phylogenies and palaeoclimatic reconstructions. We found coincidence between climatic conditions preferred nowadays and ancestral climatic conditions for the different groups of reptiles suggesting that niche conservatism is valid to interpret African reptile richness patterns.

Secondly, we investigate the extent to which evolutionary relationships between species of oscine passerine birds can explain their geographical range size patterns in the New World. Range size patterns are documented for migratory and non-migratory species and are partitioned into the portion explained by evolutionary relationships and the portion that is independent from them by using phylogenetic methods of partition of the variance. The results indicate that range size is moderately heritable for this group of birds and hence its study needs to account for the role played by evolution. Furthermore, the patterns are different for migratory and non-migratory species, supporting the effect of mesoscale climatic gradients that are found in mountainous regions. Regional differences and phylogenetic structure found in migratory ranges, suggest the convenience of including other biological traits as dispersal ability, to reach a bettern understanding of the processes conditioning the biogeography of oscine range size.

In third place, we examine the relative contributions of deep evolutionary relationships to the global bird body size gradient, distinguishing between the part of the gradient which is phylogenetically structured from the part that is independent from the phylogeny and thus might respond to adaptive phenomena under the family level. In this case, apart from the phylogenetic partition of the variance we use partial regressions to account the portions of the variance in bird body size that are explained by the phylogeny, by environmental gradients or by both simultaneously. Results show a strong effect of evolutionary relationships over the body size gradient. Also identify primary productivity either in combination with temperatura in the New World or with seasonality in the Olod World, as the primary environmental descriptor of bird body size. This supports the hypotheses of resistance to starvation and heat conservation to explain the portion of body size independent from evolutionary relationships.

Finally, we inspect the effects that historical large scale dispersal events such as the biotic exchanges occurred during the Pleistocene, might have had on the mammal body size gradient in the New World. The body size patterns of the groups of mammals that participated in the biotic exchanges of and the groups that did not participate are compared, as are their phylogenetic signals and their associations with environmental gradients. Results inform of a strong, geographically localized influence of allochthon mammals over the body size gradient of all species. We also find marked differences between the sizes of autochthons and allochthons and their phylogenetic signal or their associations with climate. These differences can be interpreted based on the more recent arrival of allochthon species to North and South America in combination with niche conservatism dynamics.

The findings of this thesis are relevant to macroecology and emphasize that including evolutionary and historical processes is key to understanding biogeographical diversity patterns. Phylogenetic relationships, ancestry and its associations with palaeoclimates, the fossil record and the biotic exchanges occurred due to palaeogeographic changes should be accounted for to bring us closer to the role of niche conservatism in configuring Earth´s biotas.

1. Introducción general

Capítulo 1

Introducción general
Patrones de diversidad en macroecología

> *'…the nearer we approach the tropics, the greater the increase in the*
> *variety of structure, grace of form, and mixture of colors,*
> *as also in perpetual youth and vigour of organic life.'*
>
> Alexander Von Humboldt (1807)

Desde que James Brown y Brian Maurer acuñaran el término 'macroecología' (ej. macroecology) en la revista Science hace ya más de veinte años (Brown y Maurer 1989), el interés suscitado por este campo de investigación no ha dejado de aumentar. Claro reflejo es el elevado número de libros, artículos científicos y congresos dedicados a éste ámbito y a otros relacionados como la Biogeografía (ej. Brown 1995; Gaston y Blackburn 2000; Hortal y Dawson 2009). La macroecología es un programa de investigación no experimental y no manipulativo que aborda el estudio de las relaciones existentes entre los organismos y entre estos y su ambiente haciendo uso de escalas espaciales y temporales extensas, con objeto de caracterizar y explicar los patrones de abundancia, distribución y diversidad de dichos organismos y de sus características biológicas (ver Brown 1995). Esta disciplina utiliza una aproximación macroscópica e inductiva (observación de patrones que son posteriormente explicados) más interesada en una visión global de los sistemas ecológicos que en las idiosincrasias propias de distintas regiones (Gaston y Blackburn 2000). En otras palabras, la macroecología mira a los ecosistemas desde fuera para encontrar patrones emergentes y explicar los procesos subyacentes, que en numerosas ocasiones no resultan obvios a escalas menores.

El estudio de algunas de las cuestiones de mayor interés para la macroecología o la biogeografía como pueden ser la variación geográfica de la riqueza de especies, del tamaño corporal o del tamaño del rango geográfico de distintas biotas, está lejos de ser algo novedoso. Por el contrario, dichas preguntas ya fueron abordadas hace más de dos siglos por parte de exploradores y estudiosos de historia natural como George Edwards, (1743), Alexander von Humboldt (1807), Alfred R. Wallace (1878) o Ernst Haeckel (1905). Desde entonces se fueron acumulando datos relativos a la distribución geográfica de las especies y se fue documentando la variación de algunas propiedades de los ecosistemas en relación al clima y la geografía. El aumento de información relativa a los gradientes biológicos globales no fue acompañado de un marco científico analítico que permitiese profundizar en el entendimiento de los patrones observados. A tal efecto, la obra de Robert H. MacArthur resultó fundamental en la sistematización de los estudios ecológicos a grandes escalas (MacArthur 1972). En "Geographical Ecology" el autor abogaba por la utilización de escalas extensas en el estudio de los gradientes de diversidad biológica, ya que éstas permiten descubrir patrones y predecir mecanismos que al mismo tiempo influencian y responden a aquello que ocurre a escalas menores. Se trataría según MacArthur, de en lugar de explicar el todo por sus partes como se había venido haciendo desde otros enfoques ecológicos (ej. poblaciones, comunidades), explicar las partes por el todo:

> *"... la mayoría de científicos creen que las propiedades del todo son consecuencia del comportamiento y las interacciones de sus componentes. Esto no quiere decir que para entender el todo haya siempre que comenzar estudiando sus partes. Podemos encontrar patrones en el todo que no son para nada evidentes en sus partes por separado." (MacArthur 1972)*

Dado que existen propiedades emergentes de los ecosistemas que no podrían explicarse a partir de las distintas partes que los componen, la investigación a escalas biogeográficas surge como un enfoque complementario para estudios a escalas menores (v.g. ecología de poblaciones, comunidades). Como en cualquier disciplina científica, un entendimiento profundo de los procesos ecológicos probablemente solo pueda alcanzarse incorporando observaciones desde un amplio rango de puntos de vista y haciendo uso de distintas escalas (Gaston & Blackburn 2000).

Por tanto uno de los principales intereses de la macroecología es el estudio de patrones de biodiversidad, o dicho de otro modo, de la variación de rasgos biológicos a lo largo de gradientes ambientales o temporales haciendo uso de escalas grandes. Ciertos patrones de la diversidad biológica han alcanzado la consideración de 'reglas' (ecogeográficas o evolutivas) cuando las tendencias se repiten de forma recurrente y las excepciones son lo suficientemente escasas (Gaston *et al.* 2008). Varios de estos patrones describen regularidades con cierto valor histórico o de autoecología de las especies, aunque no aportan información relevante acerca del funcionamiento de los sistemas ecológicos. Ejemplos son la regla de Gloger (1833), que describe una pigmentación más oscura de los individuos de una especie a medida que aumenta la humedad ambiental; o la regla de Allen (1878), que propone que la longitud de las extremidades corporales de los organismos endotermos tiende a aumentar hacia regiones cálidas. Otros ejemplos de reglas ecogeográficas, sin embargo, estudian rasgos biológicos esenciales para entender los mecanismos que influencian los patrones observados en la naturaleza. Un ejemplo sería de la regla de Foster (1963), que en ambientes insulares prevé por un lado una tendencia a la disminución del tamaño corporal de especies grandes debida a una menor disponibilidad de recursos y, por otro, una tendencia al aumento del tamaño de especies pequeñas que se enfrentarían a menores presiones de depredación. Como ejemplo de regla evolutiva cabe destacar la regla de Cope (1887) que predice que los organismos tienden a aumentar su tamaño corporal a medida que transcurre el tiempo a lo largo del cual han podido evolucionar.

Mención especial merecen tres de las reglas ecogeográficas que han sido objeto de mayor atención en la literatura científica (Gaston 2008) y en cuyo estudio se centra esta tesis doctoral. En primer lugar, el gradiente latitudinal de riqueza de especies, o la tendencia a encontrar un mayor número de especies en los trópicos. Dicho gradiente es probablemente el más antiguo y mejor conocido por los ecólogos (Hawkins 2001) desde que fuese indicado por Johann R. Forster (1778) y formalmente planteado por Alexander von Humboldt (1807). La explicación para el gradiente latitudinal de riqueza de especies, tradicionalmente relacionada con el clima y las dinámicas de agua-energía (Hawkins *et al.* 2003), tendría además que ver con procesos históricos y evolutivos de diverisficación, extinción y dispersión (Ricklefs 2007). Mecanismos como la conservación de nicho o el tiempo disponible para la especiación (ver abajo; Peterson *et al.* 1999, Stephen y Wiens 2003, Wiens y Donoghue 2004) constituyen un marco desde el que acercar posturas para alcanzar el consenso en cuanto a la explicación de un patrón que sigue siendo objeto de debate en la actualidad (Hawkins 2008).

En segundo lugar, tenemos la regla de Bergmann (1847), que afirma que dentro de grupos de endotermos con amplias distribuciones geográficas, las regiones más frías tienden a estar habitadas por especies grandes. El tamaño corporal es posiblemente el atributo de biotas animales más estudiado en la literatura ecológica y evolutiva (Gaston y Blackburn 2000) ya que constituye seguramente el mejor indicador de otros rasgos de la historia de vida de las especies (Peters 1983, Calder 1984, Harvey y Pagel 1991). Una posible explicación para esta regla (Bergmann 1847) se basa en un mecanismo de conservación de calor (debido a la menor superficie específica de las especies de mayor tamaño) y sugiere un papel significativo del tamaño corporal en la distribución geográfica de organismos endotermos. También se han propuesto hipótesis alternativas a la conservación de calor para explicar las relaciones entre los gradientes de tamaño corporal y la variación climática o ambiental (Blackburn y Hawkins 2004). Por ejemplo, la hipótesis de disponibilidad de hábitat, que sugiere la tendencia a encontrar tamaños corporales pequeños en ambientes montañosos debido a que existe una mayor zonación de hábitats y una menor extensión de cada hábitat en dichos ambientes (ver Rodríguez *et al.* 2008); o la resistencia a la escasez de recursos que prevé especies de mayor tamaño en regiones con poca productividad primaria, dado que especies grandes presentan mayores reservas lipídicas y por tanto son capaces de resistir periodos más largos de escasez de recursos (Lindsey 1966, Calder 1984). La idiosincrasia regional de los patrones y las excepciones a la regla de Bergmann, apuntan hacia la necesidad de recurrir a hipótesis históricas o evolutivas basadas bien en la influencia de las glaciaciones o los intercambios bióticos ocurridos durante el Pleistoceno (Marquet y Cofré 1999; Blackburn & Hawkins 2004; Rodríguez *et al.* 2006), en dinámicas de colonización-diversificación, o en la selección de otros caracteres asociados al tamaño corporal (Blackburn *et al.* 1999), para explicar los gradientes de tamaño corporal.

Por último, consideramos la regla de Rapoport (1982), que contempla la existencia de rangos geográficos más extensos en latitudes altas y frías que en latitudes tropicales. Una de las explicaciones más utilizadas para explicar este patrón es la hipótesis de la variabilidad climática (Stevens 1989, Lechter y Harvey 1994), que postula una mayor presencia de especies generalistas con amplios rangos de distribución en latitudes altas, ya que los organismos generalistas presentan más capacidad para tolerar la mayor variabilidad climática existente en esas latitudes. Parte de la importancia de este mecanismo es que ha sido utilizado también para explicar el gradiente latitudinal de riqueza de especies basándose en que las especies generalistas mostrarán un mayor solapamiento en sus rangos de distribución y, por exclusión competitiva, cabría esperar un menor número de especies al acercarnos a los polos. Como en los casos anteriores, no parece haber una explicación universal para los patrones de tamaño de rango (Hernández-Fernández y Vrba 2005) por lo que alcanzar un entendimiento completo de estos patrones requiere la utilización de hipótesis complementarias. A modo de ejemplos de dichas hipótesis se pueden destacar el tiempo transcurrido desde la retirada de los glaciares (Brown 1995, Rohde 1996), que habría permitido a las especies con mayores capacidades dispersoras ocupar áreas previamente ocupadas por extensas capas de hielo; o la variación en la conectividad entre distintos continentes debido a cambios paleogeográficos (Hernández-Fernández y Vrba 2005), que habrían fomentado la reconfiguración de los tamaños de rangos geográficos haciendo disponibles nuevas áreas para su colonización. Otras hipótesis susceptibles de ser estudiadas estarían relacionadas con la medida en que el tamaño de rango es una propiedad 'heredable' (Jablonsky 1987, Hunt *et al.* 2005), en cuyo caso los centros de origen de distintos clados serían importantes para determinar los gradientes de tamaño de rango geográfico.

El estudio de las reglas ecogeográficas ha sido objeto de intenso debate científico y en todos los casos existen ejemplos de excepciones a las mismas (ver Ashton 2001, Kouki *et al.* 1994, Ruggiero 1994) que han sido usadas en ocasiones para desautorizar o refutar su consideración como reglas (MacNab 1971, Gould 1997, Gaston *et al.* 1998, Meiri y Dayan 2003). Al margen de su validez o su universalidad, el estudio del gradiente latitudinal de riqueza, de la regla de Bergmann o la regla de Rapoport y, de las excepciones encontradas, contribuyen a ampliar nuestro conocimiento sobre los procesos que determinan la distribución de la biodiversidad (Zeveloff y Boyce 1988, Cotgreave y Stockley 1994, Blackburn y Gaston 1996, Blackburn y Hawkins 2004, Rodríguez *et al.* 2006, Medina *et al.* 2007). Los patrones de diversidad que hemos citado han sido estudiados durante los últimos doscientos años y actualmente nos acercamos a haber completado el primer paso del programa macroecológico; es decir, a tener un buen conocimiento de cuáles son los patrones que observamos en la naturaleza, al menos para ciertos grupos animales (Gaston y Blackburn 1999). Sabemos por ejemplo, que la riqueza de especies está fuertemente correlacionada con las dinámicas de agua-energía (Hawkins *et al.* 2003), que los gradientes de tamaño corporal se correlacionan con la temperatura (especialmente en climas fríos, ver Rodríguez *et al.* 2006, Rodríguez *et al.* 2008, Diniz-Filho *et al.* 2009, Olson *et al.* 2009) o que el tamaño de rango geográfico está correlacionado con el tamaño del territorio disponible para colonizar y con gradientes de temperatura en escalas intermedias (Rapoport 1982, Hawkins y Diniz-Filho 2006). A pesar de ello, la comunidad científica está aún lejos de esclarecer los mecanismos y los procesos subyacentes a los patrones observados. Éste es el siguiente paso a completar en el programa macroecológico y para ello será necesario integrar hipótesis evolutivas e históricas que ayuden a alcanzar explicaciones más completas sobre el funcionamiento de sistemas adaptativos complejos, como son aquellos que interesan a los ecólogos.

Evolución, historia y patrones de diversidad

> *Nothing in biology makes sense except in the light of evolution*
>
> Theodosius Dobzhansky (1973)

Durante el último siglo, la dialéctica existente entre las explicaciones ecológicas y las explicaciones históricas o evolutivas de los patrones de diversidad ha quedado patente en numerosas discusiones en la literatura científica (ver Ricklefs 2004). Si bien existe un amplio consenso en cuanto a la fuerte asociación entre los gradientes de diversidad y los factores climáticos y ambientales (Currie 1991, Hawkins *et al.* 2003), el determinismo local no es suficiente para explicar del todo las relaciones diversidad-ambiente (Ricklefs 2004). Teniendo en cuenta las diferencias existentes en los patrones de diversidad de regiones con distintas historias biogeográficas (Schluter & Ricklefs 1993) y teniendo en cuenta también, que la evolución es la causa última de la diversidad de especies así como de la diversidad de los rasgos ecológicos, fisiológicos, morfológicos o de comportamiento de los seres vivos (Wiens *et al.* 2010), parece lógica la necesidad de incluir factores históricos y evolutivos en el estudio de los patrones de diversidad. La distribución y diversidad de organismos estudiada a grandes escalas resulta por tanto de la interacción entre la historia ambiental de las regiones habitadas por esos organismos y la historia evolutiva de los linajes a los que pertenecen (Brown 1995).

En concreto, los patrones de riqueza de especies dependen en última estancia de los eventos de especiación y extinción, que están reflejados en las relaciones filogenéticas existentes entre un grupo de organismos, así como de los eventos de dispersión protagonizados por dichos organismos (Ricklefs 2004). Las condiciones climáticas y ambientales y sus variaciones a lo largo de la historia, habrían actuado como filtro determinante de las probabilidades de especiación, extinción y expansión o contracción del rango de distribución de las especies (Brown 1995). La riqueza de especies podría también estar influenciada indirectamente por la capacidad de otras propiedades emergentes (v.g. el tamaño corporal o el tamaño de rango) de prestar ventajas adaptativas o una supervivencia diferencial en determinados ambientes (Brown 1995). Por ejemplo, el tamaño corporal, fuertemente constreñido filogenéticamente

(Gittleman *et al.* 1996, Blomberg *et al.* 2003, Ramirez *et al.* 2008, Diniz-Filho *et al.* 2009; Cooper & Purvis 2010), podría explicar mayores valores de riqueza de especies de gran tamaño en ambientes fríos, si ser grande proporcionase ventajas adaptativas en esos ambientes. Igualmente, el tamaño de rango, que presenta dinámicas temporales de variación desde que las especies se originan hasta que se extinguen (Gaston 1998, Gaston & Chown 1999, Webb *et al.* 2000, Jones *et al.* 2005), podría ser seleccionado, favoreciendo por ejemplo especies con amplios rangos de distribución en ambientes de marcada estacionalidad. Además, otros factores históricos como las glaciaciones ocurridas durante el Pleistoceno (Klicka y Zink 1997), los intercambios bióticos ocurridos durante el Cenozoico tardío (Marshall *et al.* 1982, Webb y Barnosky 1989) u otros eventos de cambios climáticos ocurridos en el pasado (Svenning 2003), habrían propiciado fenómenos de dispersión de organismos con los consiguientes impactos sobre los patrones contemporáneos de diversidad.

Ante la necesidad de integrar explicaciones de los patrones de diversidad basadas en sus relaciones con factores ambientales actuales o basadas en sus relaciones con otros factores históricos y evolutivos, la conservación de nicho constituye el marco desde el que analizar las relaciones entre similitud ecológica y parentesco filogenético (Harvey y Pagel 1991, Holt 1996, Peterson *et al.* 1999, Wiens y Donoghue 2004). Éste fenómeno, predice la retención de rasgos relacionados con el nicho ecológico de las especies a lo largo del tiempo evolutivo (ver Figura 1; Wiens *et al.* 2010) y por tanto, en base a él, la maleabilidad de los nichos ecológicos de las especies y su capacidad de adaptación a condiciones cambiantes sería limitada (Peterson 2011). La conservación de nicho representa al mismo tiempo un patrón de similitud ecológica a través del tiempo evolutivo y un proceso o mecanismo. Esto sucede cuando dicha similitud genera otros patrones como por ejemplo extinciones locales o migraciones de organismos derivadas de cambios climáticos (Wiens *et al.* 2010). En la última década, la conservación de nicho ha sido la base de numerosos estudios en ecología y biología evolutiva; en primer lugar para establecer la existencia o no del fenómeno (Peterson *et al.* 1999, Losos *et al.* 2003, Wiens y Donoghue 2004, Wiens y Graham 2005, Hawkins *et al.* 2007, Wiens *et al.* 2007) y, en segundo lugar, para conocer cuáles son los atributos del nicho que se conservan y cuáles no. Es decir, para determinar qué elementos del nicho de las biotas experimentan cierta retención evolutiva y son pues susceptibles de dar lugar a fenómenos de especiación (Kozak y Wiens 2006). Más recientemente el interés se ha centrado en cuantificar la conservación de nicho, documentando su influencia sobre la distribución de las biotas y tratando de entender los modelos evolutivos que lo originan (Kozak y Wiens 2006, Buckley *et al.* 2010,

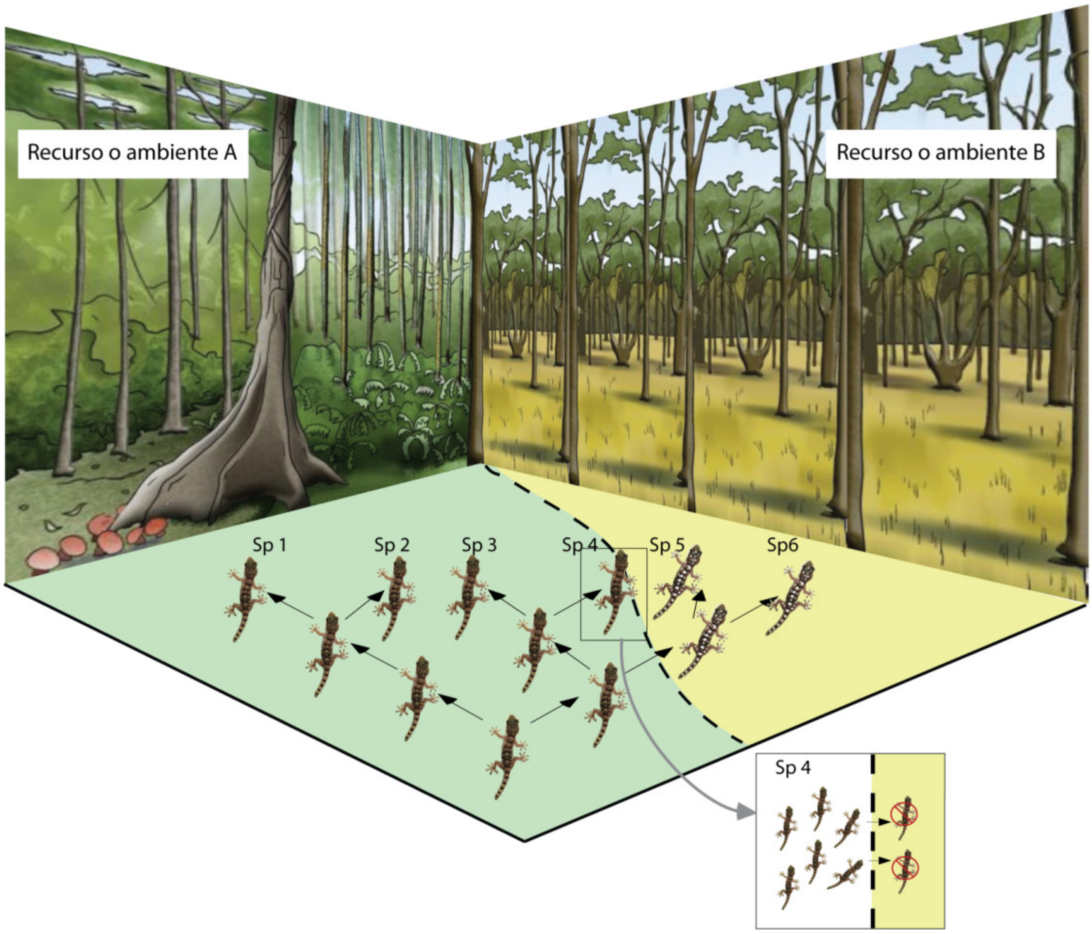

Figura 1. Ilustración de cómo la conservación de nicho puede generar patrones filogenéticos en datos ecológicos (modificado a partir de Wiens *et al.* 2010 pp. 1312). El esquema muestra la diversificación de un clado originado a partir de una especie ancestral (Sp 0) utiliza un ambiente/recurso determinado (A). La mayor parte del clado diversifica utilizando dicho ambiente/recurso originario (A) mostrando un mayor número de riqueza de especies (Sp 1-4). Ocasionalmente se produce un cambio de nicho para algún descendiente permitiéndole usar un ambiente/recurso diferente del ancestral (B). dando lugar a descendencia (Sp 5-6). Este patrón se debe a la conservación de nicho. Como se observa en el recuadro, los individuos de la Sp 4 tratando de utilizar un ambiente/recurso nuevo (B) muestran desventajas adaptativas que les dificultan usar ese nuevo nicho y por tanto conservan el nicho ancestral. Este fenómeno podría explicarse por la falta de variación genética necesaria para persistir en el nuevo ambiente, una selección que favorezca la elección del ambiente/recurso ancestral (A) o la competición con especies que ya utilizasen el recurso/ambiente nuevo (B).

Cooper *et al.* 2010, Wiens *et al.* 2010). El potencial del marco teórico que proporciona la conservación de nicho a la hora de relacionar procesos históricos y evolutivos con los patrones de diversidad actuales (Wiens y Graham 2005) justifica su presencia explícita a lo largo de esta tesis doctoral.

La conservación de nicho también ha generado debate en cuanto a su definición conceptual, o al modo en que debe analizarse (Losos 2008). Por un lado, existen estudios que miden la conservación filogenética de nicho (CFN) en base a señales filogenéticas. Estos asumen que señales filogenéticas no aleatorias, resultantes de procesos de deriva genética o selección natural que dan lugar a patrones brownianos de evolución, proporcionan evidencia de CFN (Pagel 1999, Blomberg y Garland 2002). Por otro lado, hay investigadores que opinan que la conservación de nicho se produce cuando los nichos de especies cercanas filogenéticamente se parecen más entre sí de lo que se esperaría de un modelo browniano de evolución (Blomberg *et al.* 2003, Losos 2008, Revell *et al.* 2008). Además, la conservación de nicho puede interpretarse en relación a la conservación de las tolerancias climáticas de las especies (Peterson *et al.* 1999, Wiens y Graham 2005, Hawkins *et al.* 2006), o a otras dimensiones del nicho ecológico como la dieta (Losos *et al.* 2003), el tamaño corporal, o el tamaño del rango geográfico (Cooper *et al.* 2011). Si bien no existe consenso en cuanto a cómo analizar la conservación de nicho, recientes trabajos centran la cuestión indicando qué métodos podrían ser más idóneos para cada una de las preguntas, así como las distintas aplicaciones del estudio de la conservación de nicho (Cooper *et al.* 2010, Wiens *et al.* 2010). Parece conveniente, además, que futuros trabajos profundicen en el estudio de los procesos evolutivos (ej. selección estabilizadora, transmisión direccional de genes, etc.) que dan lugar a la conservación de nicho para las biotas de distintas regiones (Losos 2008).

Finalmente, la conservación de nicho es importante por distintos motivos. En primer lugar, por su capacidad para explicar el gradiente latitudinal de riqueza de especies (Wiens y Graham 2005). Esta idea es reforzada por el 'efecto-del-tiempo-para-especiación' (Hawkins 2008), que sencillamente predice un mayor número de especies en los ambientes donde han surgido los distintos clados. Por ejemplo, el mayor número de especies en los trópicos podría deberse a que es en esos ambientes en los que se originaron la mayoría de los ancestros de las especies actuales (Stephen y Wiens 2003). En segundo lugar, basándonos en la idea de la conservación de nicho pueden predecirse los ambientes más idóneos para distintos grupos taxonómicos y de esta forma dirigir con mayor eficiencia los esfuerzos hacia la búsqueda de nuevas especies.

Éste es el caso de la descripción de nuevas especies de camaleones en Madagascar, que fueron encontradas mediante la modelización de los nichos de especies cercanas (Raxworthy *et al.* 2003). Además, la conservación de nicho resulta de interés porque gran parte de los estudios sobre la influencia del cambio climático en la futura distribución de especies, o las predicciones de futuras extinciones debidas a este u otros fenómenos utilizan modelos de distribución que asumen una perfecta conservación de los nichos de las especies (ej. Peterson *et al.* 1999, Araújo *et al.* 2005). Por tanto, profundizar en nuestro conocimiento sobre el grado en que los organismos conservan sus nichos, permitirá en un futuro realizar predicciones más ajustadas de los riesgos de extinción o de posibles desplazamientos de especies ante distintos escenarios de cambio global.

Análisis filogenéticos

Las relaciones evolutivas que existen entre un grupo de organismos pueden resumirse en los árboles filogenéticos que contienen información relevante a los fenómenos de especiación, en algunos casos de extinción y cada vez con más frecuencia incluyen los periodos temporales en que dichos fenómenos ocurrieron (Losos 2011). Gracias al desarrollo de la biología molecular y las técnicas de secuenciación genética (ej. Polymerase Chain Reaction, PCR), existe una creciente disponibilidad de secuencias de ADN y/o aminoácidos a partir de las cuales generar árboles filogenéticos cada vez con más especies, permitiéndonos entender cómo han tenido lugar algunos de los fenómenos que han propiciado la diversidad biológica que encontramos en la Tierra.

El perfeccionamiento de las filogenias ha ido ligado al desarrollo de técnicas de análisis estadístico, que desde hace unos 25 años han visto crecer su popularidad hasta el punto en que es difícil concebir hoy en día trabajos de biología comparada que no tengan en cuenta las relaciones filogenéticas de los organismos estudiados. Inicialmente este tipo de análisis surgieron de la preocupación por la dependencia filogenética existente entre especies y su influencia en los test estadísticos. De esta forma nacía el método filogenético comparado, que permitía comparar caracteres fenotípicos de distintas especies dadas sus relaciones evolutivas (Harvey y Pagel 1991). En otras palabras, las especies a analizar no pueden ser consideradas como unidades independientes ya que especies más cercanas evolutivamente tenderán a mostrar un mayor parecido en sus rasgos biológicos, generando autocorrelación filogenética y haciendo necesario controlar el consecuente efecto sobre el error tipo I de los análisis estadísticos (Chevereud *et al.* 1985, Felsenstein 1985, Pagel 1999, Harvey y Pagel 1991). Posteriormente, el potencial de estos análisis hizo que la atención se centrara en investigar los patrones de diversificación, la validez de distintos modelos evolutivos, la co-evolución o los estados ancestrales de distintos atributos biológicos. Así, la señal filogenética se reconoció como una métrica capaz de informar acerca de los distintos mecanismos evolutivos (ej. Maddison 1995, Diniz-Filho *et al.* 1998, Martins *et al.* 2002, Blomberg *et al.* 2003). Más recientemente, otras preguntas situadas en la interfase entre macroecología y macroevolución han cobrado importancia. Entre ellas destacan la separación de los efectos ecológicos y evolutivos sobre rasgos biológicos (Desdevises *et al.* 2003, Diniz-Filho *et al.* 2007, Diniz-Filho y Bini 2008, Freckleton *et al.* 2009, Kühn *et al.* 2009), entender cómo y/o cuándo han evolucionado esos rasgos (Cooper y Purvis 2010; Smith *et al.* 2010), comprobar si un determinado rasgo relacionado con el nicho se conserva filogenéticamente (Wiens *et al.* 2010, Cooper et al 2011, Olalla-Tárraga *et al.* 2011), así como explorar la validez de reglas ecogeográficas (e.g. Ramirez *et al.* 2008; Diniz-Filho *et al.* 2009; Olalla-Tárraga *et al.* 2010).

Existen principalmente dos grupos de métodos filogenéticos con los que explorar dichas cuestiones. Por un lado, los métodos de contrastes filogenéticos independientes (Felsenstein 1985), que partiendo del modelo de movimiento browniano, tratan de determinar cómo se ajusta o se desvía de este modelo la evolución de los caracteres objeto de estudio. Estos métodos traducen las relaciones filogenéticas a matrices de varianza-covarianza filogenética, que son incorporadas en los estudios comparados haciendo uso de algoritmos de mínimos cuadrados generalizados (GLS) para ajustar los parámetros que cuantifican la señal filogenética (ej. λ, δ; Pagel 1999). Los contrastes filogenéticos independientes son métodos basados en procesos; es decir, asumen *a priori* un modelo evolutivo frente al cual comparar los resultados y cuyo objetivo es encontrar el modelo evolutivo que mejor explica los datos (Freckleton *et al.* 2002).

Por otro lado están los métodos basados en patrones de partición de la variación. Estos hacen uso bien de modelos autorregresivos (Chevereud *et al.* 1985) o de modelos de regresión de autovectores filogenéticos (PVR, Diniz-Filho *et al.* 1998). La lógica de estos métodos consiste en separar la proporción de la variación del rasgo biológico estudiado que está correlacionada con las relaciones filogenéticas, de la proporción que es independiente de las mismas. Las relaciones filogenéticas en este caso vienen representadas por matrices de distancias filogenéticas entre pares de especies. En el caso de los modelos autorregresivos se extrae un parámetro autorregresivo que representa la autocorrelación filogenética (i.e. ρ; Chevereud *et al.* 1985) mientras que en el caso de PVR se extrae un conjunto de autovectores filogenéticos que son incluidos en una regresión de mínimos cuadrados (ver Figura 2 para más detalles). Además, dado que la señal filogenética puede interpretarse como un fenómeno de autocorrelación, los patrones filogenéticos pueden explorarse usando medidas estadísticas como el índice de autocorrelación I de Moran (Gittleman y Kot 1990), que informa de la variación de la señal filogenética a distintas profundidades de la filogenia (Martins *et al.* 2002).

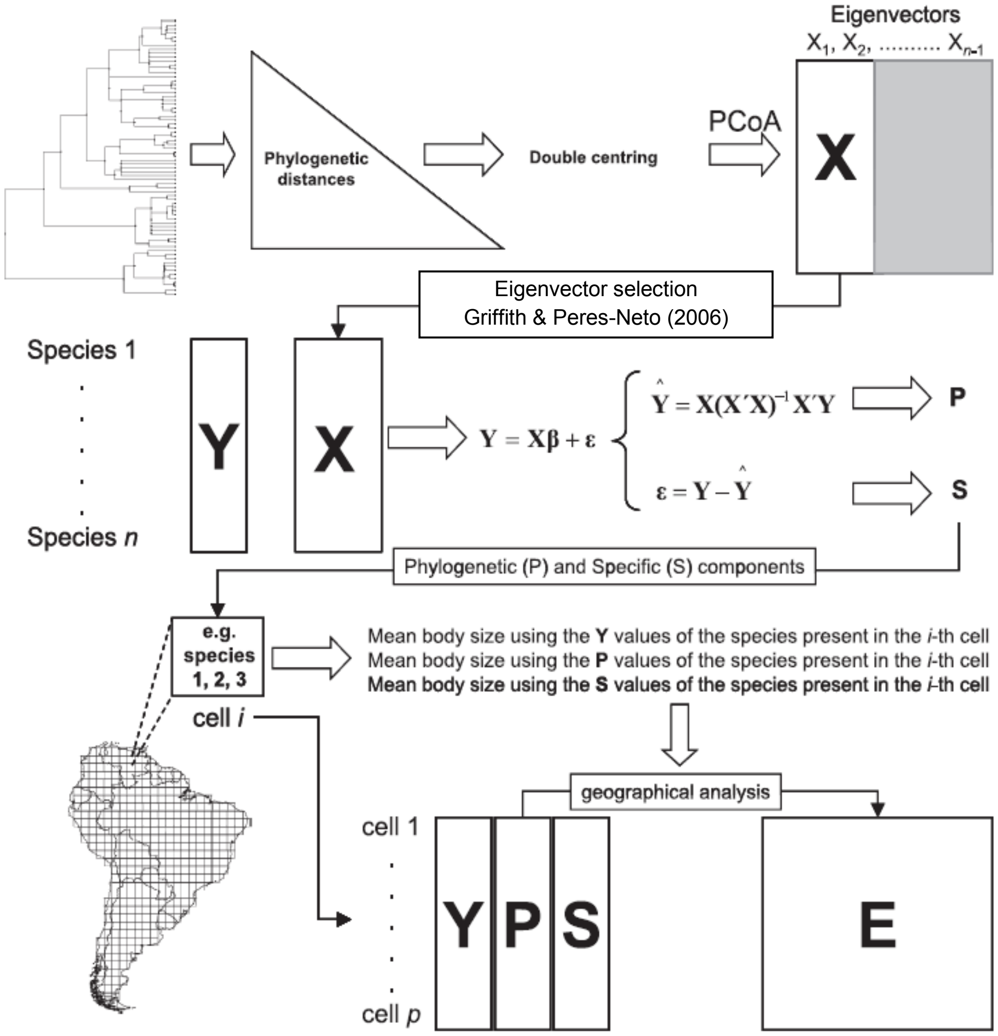

Figura 2. Esquema explicativo de la metodología de PVR, modificado de Diniz-Filho *et al.* (2009). La filogenia se expresa como una matriz de distancias filogenéticas por pares de especies, que es posteriormente descompuesta mediante PCoA a un conjunto de autovectores. De estos se selecciona un subconjunto (X) capaz de minimizar la autocorrelación residual (S) utilizando el algoritmo propuesto por Griffith & Peres-Neto (2006). Los autovectores seleccionados (X) son finalmente utilizados como variables independientes en una regresión múltiple que separa la proporción de la varianza del rasgo biológico estudiado (Y) en una componente filogenética (P) y en una componente independiente de las relaciones filogenéticas (S). Ambas componentes pueden ser promediadas para cada celda del análisis y utilizadas en análisis geográficos frente a distintas variables ambientales (E).

Aunque los métodos filogenéticos utilizan originalmente aproximaciones 'entre-especies' (*cross-species analyses*; ver abajo) dado que fueron diseñados para realizar comparaciones interespecíficas, los métodos de partición de la variación presentan la ventaja de poder ser traducidos de forma sencilla a un contexto geográfico (Diniz-Filho *et al.* 2011). Es decir, es posible crear mapas representando la variación geográfica en las componentes filogenética y no-filogenética de un rasgo biológico dado, como por ejemplo el tamaño corporal (Ramírez *et al.* 2008, Diniz-Filho *et al.* 2009). Dado que los fenómenos históricos y evolutivos tienen lugar en contextos geográficos, ser capaces de determinar cuál es la estructura espacial de los componentes evolutivos y/o históricos de los patrones de diversidad es una pregunta fundamental de muchas investigaciones. Conocer la estructura espacial de las componentes evolutiva e independiente de la variación de una propiedad biótica permite profundizar en la explicación de los patrones biogeográficos y macroecológicos, estableciendo en qué regiones la influencia de la evolución y la Historia tienen una mayor prevalencia. En otras palabras, este tipo de análisis evolutivos en contextos geográficos permitirían por ejemplo, determinar en qué regiones la variación de un rasgo biológico es independiente de las relaciones filogenética y, por tanto, podría estar más relacionado con efectos adaptativos. Estas ventajas, además de la alta correlación con los resultados de otros métodos filogenéticos (Diniz-Filho *et al.* 2011), apoyan la utilización de PVR en esta tesis doctoral.

La aproximación de ‘ensamblaje’

La aproximación de ‘ensamblaje’ es uno de los dos enfoques utilizados para realizar estudios interespecíficos de patrones de diversidad, junto a la aproximación ‘entre-especies’ (Gaston *et al.* 2008, Olalla-Tárraga *et al.* 2010). Los estudios basados en ensamblaje utilizan mallas de celdas superpuestas al área de estudio para explorar la variación geográfica de los patrones. Esta es una forma de transformar en discreta la realidad continua que se encuentra en la naturaleza, para así tener en cuenta las presencias y ausencias de todas las especies que componen el ensamblaje faunístico contenido en cada celda. Además de permitir calcular la riqueza de especies en cada celda, mediante esta metodología pueden calcularse valores promedio de otros rasgos biológicos de los ensamblajes como el tamaño corporal o el tamaño del rango geográfico (ver figura 3 para más detalles sobre el método). En las celdas, que son utilizadas como unidades de análisis, pueden además promediarse los valores para los distintos descriptores ambientales y de esta manera es posible analizar las asociaciones entre los patrones geográficos de diversidad y los gradientes ambientales.

El enfoque ‘entre-especies’ por el contrario, utiliza cada una de las especies incluídas en un estudio como unidad de análisis. En este caso, a cada especie se le asocia su valor para el rasgo biológico objeto de estudio y, por otro lado, se obtienen valores promedio de la variación ambiental existente en todo su rango de distribución geográfica (Gaston *et al.* 2008). Estos valores promedio, pueden referirse a descriptores ambientales o al posicionamiento geográfico de cada especie (generalmente el punto latitudinal medio de su área de distribución). Posteriormente los análisis, correlaciones o modelos, se calculan a partir de los dos tipos de valores. Este tipo de enfoque a menudo se utiliza sin tener en cuenta el contexto geográfico explícito en que ocurren las especies estudiadas (ej. Ricklefs *et al.* 2007).

Una ventaja del enfoque de ensamblaje es que se puede evaluar directamente la estructura ambiental que subyace a los patrones biogeográficos. Frente a la limitación de los análisis ‘entre-especies’ que simplifican toda la variación existente dentro del rango de distribución de las especies, a una única métrica (Blackburn y Hawkins 2004, Ruggiero y Hawkins 2006). A pesar de esto, existen numerosos y recientes estudios que escogen enfoques ‘entre-especies’ para realizar estudios de patrones espaciales y evolutivos (Freckleton y Jetz 2009, Cooper *et al.* 2011, Freckleton *et al.* 2011, Adams y Church 2011). Existe también un fuerte debate sobre la conveniencia de una aproximación sobre la otra (Olalla-Tárraga *et al.* 2010, Adams y Church 2011), aunque es posible que la idoneidad de los métodos dependa más de las preguntas que quieren responderse que de las virtudes y defectos de los propios métodos. Si bien es cierto que los estudios 'entre-species' son muy utilizados en contextos puramente filogenéticos, los procesos ecológicos y evolutivos responsables de generar patrones de diversidad ocurren en contextos geográficos. Dado que esta tesis se centra en la descripción y explicación de patrones espaciales de diversidad, se favorece el uso de enfoques espacialmente explícitos basados en ensamblaje, tal y como ha sido recomendado por numerosos autores (Blackburn y Hawkins 2004, Ruggiero y Hawkins 2006).

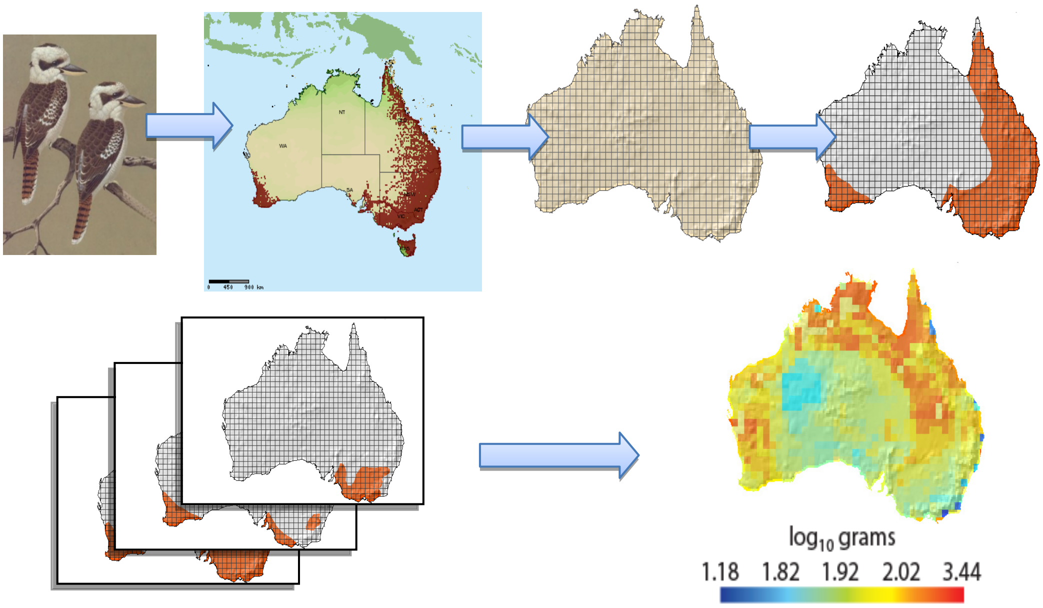

Figura 3. Procedimiento de la metodología de ensamblaje. Partiendo de mapas de la distribución de las especies, estos se traducen a una malla de celdas (las celdas de aproximadamente 1° de latitud x 1° de longitud son comúnmente utilizadas en macroecología). Posteriormente los mapas con las celdas en que las especies están presentes son superpuestos y pueden obtenerse valores de riqueza de especies, o calcularse valores medios de tamaños corporales, tamaños medios de rango u otros rasgos biológicos para la comunidad de especies presentes en cada celda.

Objetivo general de la tesis doctoral

El objetivo general de esta tesis doctoral es describir y explicar patrones biogeográficos de la diversidad de vertebrados terrestres, examinando sus relaciones con factores ambientales actuales e históricos, así como con la historia evolutiva de las faunas objeto de estudio. Aunque el objetivo puede parecer extenso, el foco de interés reside en subrayar la importancia de los factores históricos y evolutivos en el estudio de estos patrones empleando cuatro casos de estudio. En cada caso se hace uso de distintas metodologías y distintos grupos de vertebrados, con objeto de investigar cómo, la evolución y la historia afectan a los patrones de diversidad. La conservación de nicho constituye el marco desde el que se interpretan las relaciones existentes entre evolución/historia y patrones de diversidad. En concreto, los organismos objeto de estudio son distintos grupos de vertebrados terrestres (reptiles, aves y mamíferos), pertenecientes a distintas áreas geográficas. Por otra parte, los patrones de diversidad estudiados se corresponden con aquellos que han provocado un mayor interés en el campo de la macroecología, es decir, la riqueza de especies, el tamaño corporal y el tamaño de rango geográfico.

Estructura y objetivos específicos

Esta tesis doctoral está estructurada en seis capítulos. Tras este capítulo introductorio, se presentan cuatro capítulos en inglés en formato de artículos científicos, con sus correspondientes secciones de introducción, material y métodos, resultados y discusión, todos ellos precedidos de un resumen en castellano e inglés. Estos capítulos reproducen los contenidos de artículos o bien publicados (Capítulo 2), en revisión (Capítulo 3) o preparados para ser enviados a revistas científicas (Capítulos 4 y 5). Por último, el Capítulo 6 expone las conclusiones generales de la tesis doctoral. Cada capítulo tiene su propia sección de referencias bibliográficas y los apéndices oportunos. A continuación pueden verse el fundamento científico y los objetivos concretos de cada capítulo de investigación. Un resumen de los mismos se presenta también en la Tabla 1.

Tabla 1. Estructura de la tesis doctoral indicando el contenido, el objeto de estudio, el contexto geográfico, el grupo taxonómico estudiado o los resultados obtenidos de cada uno de los cuatro capítulos de investigación.

	Patrón de diversidad estudiado	**Contexto geográfico**	**Grupo taxonómico**	**Resultados**
Capítulo 1	Introducción general			
Capítulo 2	Riqueza de especies	Este y Sur de África	Reptiles escamados	Morales-Castilla *et al.* (Austral Ecology)
Capítulo 3	Tamaño del rango geográfico	Nuevo Mundo	Aves Paseriformes	Hawkins *et al.* (en preparación)
Capítulo 4	Tamaño corporal	Global	Aves	Morales-Castilla *et al.* (en revisión)
Capítulo 5	Tamaño corporal	Nuevo Mundo	Mamíferos terrestres	Morales-Castilla *et al.* (en preparación)
Capítulo 6	Conclusiones generales			

Capítulo 2. *Conservación de nicho y patrones de riqueza de especies de reptiles escamados en el Este y el Sur de África*

Cuando se estudia la diversidad biológica de distintas regiones a gran escala, ésta responde a las condiciones climáticas actuales, pero también a los centros geográficos donde se originaron las especies y a las respuestas evolutivas a cambios ambientales ocurridos durante la historia de las biotas (Hawkins *et al.* 2003, Currie *et al.* 2004, Mittelbach *et al.* 2007, Wiens *et al.* 2007).

El mecanismo que propone la conservación de nicho, es decir, la retención de las características ecológicas de las biotas a lo largo de su evolución, predice que las condiciones ambientales preferidas por las especies en la actualidad, tienden a ser similares a las condiciones que predominaban cuando se originaron sus ancestros (Holt 1996, Peterson *et al.* 1999, Wiens and Donoghue 2004, Wiens and Graham 2005). Se han encontrado multiples evidencias de la validez de este mecanismo para distintos grupos taxonómicos como por ejemplo, aves (Peterson *et al.* 1999, Hawkins *et al.* 2007), anfibios (Kozak y Wiens 2006, 2010) o mamíferos (Martínez-Meyer *et al.* 2004, Buckley *et al.* 2010), frecuentemente referidos a la conservación de nichos tropicales. De ser cierto este mecanismo, las señales de conservación de nicho deberían poder encontrarse también para organismos originados en ambientes extra-tropicales.

En este contexto el capítulo se propone documentar los patrones de riqueza de especies de cinco grupos de reptiles escamados en África (objetivo 1), explorar las relaciones existentes entre la riqueza de especies de esos grupos y el clima actual (objetivo 2) y finalmente se pretende responder a si las relaciones riqueza-clima actuales reflejan las condiciones ambientales ancestrales ante las que los grupos se originaron, ya sean estas tropicales o extra-tropicales (objetivo 3).

Capítulo 3. *Geografía de las señales filogenética y no-filogenética del tamaño de rango de paseriformes oscines (Aves) del Nuevo Mundo*

Establecer el grado en que la macroevolución ha influenciado los tamaños del rango de distribución de las especies es una cuestión que se ha investigado ampliamente (ej. Jablonski 1987, Gaston 1998, Webb y Gaston 2003) y para la cual aún no existen respuestas claras. Distintos estudios han encontrado niveles reducidos de heredabilidad para este rasgo biológico, lo que en cierto modo es lógico debido a las mayores dinámicas temporales del tamaño de rango en comparación a otros rasgos. Es decir, las especies expanden y contraen sus rangos de distribución a lo largo de sus historias evolutivas (Gaston 1998, Gaston y Chown 1999, Webb *et al.* 2000), algo que no ocurre por ejemplo, con el tamaño corporal. En cualquier caso, la alta correlación del tamaño de rango con otras características de las biotas (ej. Pocock *et al.* 2006) que sí muestran una fuerte conservación filogenética hace prever cierto grado de heredabilidad.

Dado que aún estamos en proceso de conocer los patrones en la señal evolutiva en el tamaño de rango de las especies, este capítulo se propone analizar el grado de heredabilidad del rango geográfico para el subgrupo de aves paseriformes oscines (objetivo 1). Más importante aún, debido a que la existencia de estructura espacial en la señal filogenética del rango geográfico ha sido escasamente estudiada (Machac *et al.* 2011), y que el tamaño de rango geográfico es esencialmente espacial, se pretende documentar los patrones espaciales de las componentes filogenética y no filogenética del tamaño de rango (objetivo 2). Finalmente, estudiar dichos patrones para un grupo taxonómico extremadamente móvil como las aves, que presenta migraciones estacionales permite analizar las diferencias entre los rangos migratorios y los rangos reproductivos (objetivo 3).

Capítulo 4. *Filogenia basal, productividad primaria y el gradiente global de tamaño corporal de aves*

Estudios recientes han demostrado la validez de la regla de Bergmann en aves para el Nuevo Mundo y a escala global (Ramirez *et al.* 2008, Olson *et al.* 2009, respectivamente). Los mecanismos responsables de estos patrones sin embargo, siguen siendo objeto de debate y el número de hipótesis propuestas para estudiar la variación geográfica del tamaño corporal es extenso (Blackburn *et al.* 1999). Entre ellas, se ha propuesto la alternancia espacial de grupos taxonómicos, derivada de la diversificación diferencial de clados con distintos tamaños corporales, como posible causa evolutiva de los patrones (Olson *et al.* 2009). Ésta y otras hipótesis históricas, como la colonización diferencial de áreas de las que se retiraron los glaciares tras el Pleistoceno (Blackburn and Hawkins 2004), no se han estudiado utilizando análisis filogenéticos explícitos y por tanto se han utilizado como explicaciones '*ad hoc*' para los patrones observados.

Por otro lado, el estudio de hipótesis ecológicas basadas en respuestas adaptativas de las especies ante distintos gradientes ambientales deberían estudiarse teniendo en cuenta la correlación filogenética para rasgos biológicos conservados evolutivamente como el tamaño corporal (Diniz-Filho *et al.* 2009). Parece también interesante la posibilidad de cuantificar las aportaciones independientes y conjuntas de ecología y evolución para explicar la variación del tamaño corporal definiendo qué partes corresponden a inercia filogenética, a conservación de nicho o a la variación ambiental independientemente de la evolución (Desdevises *et al.* 2003).

En este capítulo se trata de explorar el grado en que el tamaño corporal de aves está restringido por niveles profundos de la filogenia (nivel de familia) analizando la distribución geográfica de las componentes filogenética y no filogenética del tamaño corporal de aves a escala global (objetivo 1). Se pretende también cuantificar el apoyo relativo que reciben distintas hipótesis ecológicas (ej. conservación del calor, disponibilidad de recursos, resistencia a la escasez, o competición interespecífica) para explicar la componente no filogenética del tamaño corporal (objetivo 2) y finalmente comparar las contribuciones relativas de factores ambientales y evolutivos para explicar la variación del tamaño corporal de aves (objetivo3).

Capítulo 5. *Huella de las migraciones cenozoicas y la historia evolutiva en el gradiente biogeográfico de tamaño corporal de mamíferos del Nuevo Mundo*

Entender si el tamaño corporal de las biotas es una respuesta adaptativa de las mismas a los gradientes ambientales a lo largo de su evolución, o si por el contrario está restringido por la pertenencia a clados de tamaños distintos con tendencia a conservar esos tamaños es una de las cuestiones básicas en el estudio del tamaño corporal (ej. Scholander *et al.* 1950, Palkovacs 2003, Diniz-Filho *et al.* 2009, Stillwell 2010, Yom Tov y Geffen 2011). Los estudios a escalas macroecológicas sobre estas cuestiones (Ramirez *et al.* 2008, Diniz-Filho *et al.* 2009) han asumido que los organismos estudiados han permanecido históricamente en sus distribuciones actuales y por tanto, los fenómenos adaptativos habrían ocurrido '*in situ*'. Esto podría no ser cierto debido a las grandes migraciones o intercambios bióticos ocurridos a consecuencia de cambios paleogeográficos y paleoclimáticos durante el Pleistoceno. En concreto, conocemos que un elevado número de géneros de mamíferos cruzaron el estrecho de Behring (Webb y Barnosky 1989) y un número aún mayor cruzó el Istmo de Panamá (ej. Woodburne *et al.* 2006). Si estos géneros tuvieran una influencia notable en los patrones de tamaño corporal contemporáneos, como ha sido puesto de manifiesto para Sudamérica (Marquet y Cofré 1999), es posible que parte de las supuestas respuestas adaptativas no fuesen tales, y se debieran más a efectos de la restricción filogenética sobre el tamaño corporal en clados con grandes capacidades dispersoras y tamaños corporales fuertemente conservados.

Con estos antecedentes, el capítulo se propone determinar los patrones de tamaño corporal de los grupos de mamíferos que participaron o no en los mencionados intercambios bióticos (objetivo 1), estudiar la influencia de las especies *alóctonas* sobre el patrón de todas las especies (objetivo 2) y analizar las diferencias existentes entre los grupos de especies autóctonas y alóctonas así como las posibles causas de esas diferencias (objetivo 3).

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2. Niche Conservatism in species richness of African reptiles

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Capítulo 2

Conservación de nicho y patrones de riqueza de especies de reptiles escamados en el Este y el Sur de África

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

MORALES-CASTILLA, I., OLALLA-TÁRRAGA, M. Á., BINI, L. M., DE MARCO JR, P., HAWKINS, B. A. and RODRÍGUEZ, M. Á. (2011) Niche conservatism and species richness patterns of squamate reptiles in eastern and southern Africa. Austral Ecology, 36: 550–558.

Resumen

La conservación de nicho se ha propuesto como un mecanismo clave en la determinación de los patrones de riqueza taxonómica a gran escala. En este estudio hemos documentado los patrones de riqueza de especies de cinco grupos monofiléticos de reptiles escamados (gekkonidos, cordílidos-escincidos, lacértidos, camaleones y serpientes aletinofidias) en el Este y el Sur de África con el objetivo de investigar si los patrones observados reflejaban procesos de conservación de nicho. También hemos cuantificado la riqueza de los distintos grupos y sus relaciones con las condiciones climáticas actuales, trasladando los mapas de distribución de las especies a una malla de 110 x 110 km. Además, hemos utilizado filogenias datadas y reconstrucciones paleoclimáticas en combinación con información del registro fósil, para aproximar las áreas y las características climáticas ante las que cada grupo se originó y/o radió. Con objeto de establecer las preferencias climáticas de cada grupo, se emplearon valores medios de riqueza de especies y sus intervalos de confianza corregidos geográficamente. En promedio, la riqueza de especies de grupos antiguos (gekkónidos, cordílidos-escíncidos, lacértidos) fue menor en climas ecuatoriales y mayor en climas áridos y templados, mientras que grupos más recientes (camaleones y serpientes aletinofidias) mostraron mayor riqueza en climas ecuatoriales y templados y menor riqueza ante

condiciones áridas. Todos los grupos mostraron los mayores valores de riqueza de especies en áreas con características climáticas similares a las que prevalecían cuando los grupos se originaron/radiaron. La coincidencia entre los climas actuales donde los grupos de reptiles son más ricos en especies y los climas pasados en los cuales los grupos se originaron es consistente con una explicación de los gradientes de diversidad basada en la conservación de nicho.

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Niche conservatism and species richness patterns of squamate reptiles in eastern and southern Africa

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Abstract Niche conservatism has been proposed as a mechanism influencing large-scale patterns of taxonomic richness. We document the species richness patterns of five monophyletic squamate reptile groups (gekkonids, cordylids-scincids, lacertids, chameleons and alethinophidian snakes) in eastern and southern Africa, and explore if observed patterns reflect niche conservatism processes. We quantified richness and its relationships with current climatic conditions by gridding species' range maps at 110 × 110 km. Also, dated phylogenies and palaeoclimatic reconstructions, coupled with evidence from the fossil record, were used to approximate the areas and climate characteristics in which each group originated and/or radiated. Mean species richness and geographically corrected confidence intervals in current climate types were calculated for each group in order to establish their climatic preferences. On average, the species richness of older groups (gekkonids, cordylids-scincids and lacertids) was lower in equatorial climates and higher in arid and temperate conditions, whereas more recent groups (chameleons and alethinophidian snakes) were richer in equatorial and temperate climates and less rich in arid conditions. Across all groups, higher richness was associated with climatic characteristics similar to those prevailing at the time in which each group originated/radiated. The congruence of the current climates where reptile groups are richer and the past climates amidst which those groups originated is consistent with an explanation for their diversity gradients based on niche conservatism.

Key words: African biodiversity, diversity gradient, niche conservatism, palaeoclimate, reptile, richness patterns, Squamata.

INTRODUCTION

Broad-scale diversity gradients are the product of current climatic conditions, the location of centres of origin, and ecological and evolutionary responses to long-term environmental changes (Currie 1991; Ricklefs & Schluter 1993; Hawkins *et al.* 2003; Currie *et al.* 2004; Mittelbach *et al.* 2007; Wiens *et al.* 2007; Araújo *et al.* 2008; Hawkins 2008; Hortal *et al.* 2008). In particular, niche conservatism is becoming increasingly invoked to explain global diversity gradients (Hawkins 2008). This mechanism, also referred to as phylogenetic inertia, describes the conservation of biological and ecological traits among species as groups radiate, and with respect to climate tolerances it makes the testable prediction that extant species tend to be distributed in similar environments to those where their group originated, because of difficulties in adapting to new climatic conditions (Peterson *et al.* 1999; Wiens & Donoghue 2004; Wiens & Graham 2005; Nogués-Bravo *et al.* 2008). Furthermore, clades will have occupied original habitats for longer than novel habitats; hence groups have had more time for species accumulation where they first appeared (Stephens & Wiens 2003; Hawkins 2008). These patterns have been found in turtles, birds and frogs (e.g. Stephens & Wiens 2003; Wiens *et al.* 2006; Hawkins *et al.* 2006, 2007).

Here we focus on eastern and southern Africa and document the species richness patterns of several clades of Squamata, the most species-rich order of living reptiles (Ricklefs *et al.* 2007). Africa represents a hot-spot of reptile diversity, and we selected these two disjunct areas because of the availability of detailed species distribution maps. These areas also include a representation of most of the climates found in Africa. The richness of several groups of reptiles has been shown to vary with climate in many parts of the world,

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including Europe (Rodríguez *et al.* 2005; Olalla-Tárraga *et al.* 2006), the former USSR (Terent'ev 1963), North America (Schall & Pianka 1978; Olalla-Tárraga *et al.* 2006), Australia (Pianka & Schall 1981), the Kalahari Desert (Pianka 1971), Brazil (Costa *et al.* 2007) and globally (Terribile *et al.* 2009). In general, reptile richness is positively associated with temperature or solar radiation because reptiles are extreme solar ectotherms, which differentiates them from other vertebrate groups (see Whittaker *et al.* 2007). However, in tropical and subtropical latitudes, reptile richness generally has weaker relationships with energy variables (Pianka 1971; Pianka & Schall 1981; Costa *et al.* 2007; Ricklefs *et al.* 2007; Terribile *et al.* 2009).

Here we do not generate climate-richness models. Rather, we ask whether the richness of five squamate groups that originated at different times and in different macroclimatic conditions has preserved their ancestral climatic niches with respect to richness patterns. Specifically, for each lineage, we mapped its current species richness distribution in eastern and southern Africa and then examined if higher richness occurred in climates that are similar to those prevailing at the time (and, when possible, approximate place) of a group's origin. If so, this constitutes evidence that niche conservatism has influenced the current richness patterns of that clade and suggests that niche conservatism plays a significant role in the current diversity gradients of reptiles.

METHODS

Richness patterns

Range maps for native squamate reptiles were digitized from two field guides (Spawls *et al.* 1997; Branch 1998) covering 12 countries of southern and eastern Africa (i.e. Kenya, Tanzania, Rwanda, Burundi, Uganda, Namibia, Botswana, Zimbabwe, South Africa, Lesotho, Swaziland and southern Mozambique). Species range maps were then rasterized in ArcGIS in two equal-area grids, one comprising 456 cells of 110 × 110 km each that was used for analysis, and the other comprising of 8224 cells of 27.5 × 27.5 km that was used for mapping (richness maps also shown at 110 × 110 km resolution, see Appendix S3). Species richness for each cell was obtained by superimposing the individual species' range maps. Range maps are commonly used to study richness gradients, and the patterns they generate are very similar to those generated by other data sources at moderate to large scales (Hawkins *et al.* 2008; Hortal 2008). As our data sources were more than 10 years old, we also incorporated data from more recent sources (e.g. Mariaux & Tilbury 2006; Alexander & Marais 2007; Tolley & Burger 2007; Mariaux *et al.* 2008) to update distributions and incorporate newly described species.

Squamates were divided into five monophyletic lineages according to recent squamate molecular phylogenies (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009): gekkonids (Gekkonidae, 137 species); cordylids-scincids (Cordylidae and Scincidae, 144 species); lacertids (Lacertidae, 50 species); chameleons (Chamaeleonidae, 70 species); and alethinophidian or typical snakes (Viperidae, Boidae, Pythonidae, Colubridae, Natricidae, Lamprophiidae and Elapidae, hereafter snakes, 263 species). We excluded lineages with less than 20 species in the study region (Agamidae, Varanidae, Gerrhosauridae); the scolecophidian snakes (Typhlopidae and Leptotyphlopidae) were excluded because of both phylogenetic uncertainty regarding their origin and their fossorial nature. We used the taxonomy of Uetz (2009).

Data on past and current climates

For current climates we used the update of the Köppen–Geiger Climatic Classification (Köppen 1936) recently developed by Kottek *et al.* (2006), which defines climate types according to temperature and precipitation regimes. We digitized the eastern–southern African portion of Kottek *et al.*'s (2006) map, and each of our 456 analysis cells was assigned the dominant climate class within it. There are 14 Köppen–Geiger climate types in the study area (see Appendix S1), but we excluded two ('warm temperate climate with dry summer, warm' and 'warm temperate with dry summer, hot,' in Köppen–Geiger's terminology) because they covered very small areas in the study region and neither of them was the most representative climate of any cell. The 12 climate types used for analysis and both their total area and percentage area in eastern–southern Africa were summarized in Table 1.

Based on dated phylogenies (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009), we focused on the distribution of palaeoclimates in three relevant periods for squamate evolution: (i) early to late Jurassic for the divergence of gekkonids, cordylids-scincids and lacertids; (ii) early to late Cretaceous as the divergence period for chameleons and alethinophidian snakes; and (iii) the Eocene to Miocene, when major radiations of snake families and chameleon clades occurred (see also Raxworthy *et al.* 2002; Tolley *et al.* 2008). Accordingly, we obtained palaeoclimatic maps corresponding to these periods (Upchurch *et al.* 1998; Scotese *et al.* 1999; Rees *et al.* 2000; Scotese 2002; Ziegler *et al.* 2003) and rasterized them to calculate the percentage area occupied by each climate in both Africa and the world at each period. As these maps are based on the basic Köppen–Geiger types of climates (e.g. see Upchurch *et al.* 1998 for details), they provide an approximation of the major climatic characteristics during each relevant evolutionary event that can be compared with the distribution of current climate types.

Analysis

For each lineage, climatic preferences were initially explored by averaging the species richness of the cells corresponding to each climate type and then constructing a histogram of the mean values. Higher mean richness per cell in a particular climate type would suggest a preference of the lineage for that climate type. Also, 95% confidence intervals for the mean richness values were obtained to compare mean richness among climate types. For this we took into account that our

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Table 1. Major types and subtypes of Köppen–Geiger climates in eastern and southern Africa

Köppen–Geiger climate type and subtype	Kottek *et al.*'s code	Code used here	Area (km^2)	Area (%)
Arid	B	A	3 025 000	54.8
Desert cold	BWk	Ad1	290 400	5.3
Desert hot	BWh	Ad2	641 300	11.6
Steppe cold	BSk	As1	290 400	5.3
Steppe hot	BSh	As2	1 802 900	32.6
Warm temperate	C	T	769 598	13.9
Fully humid hot	Cfa	Th1	60 500	1.1
Fully humid warm	Cfb	Th2	181 500	3.3
Dry winter, hot	Cwa	Td1	193 600	3.5
Dry winter, warm	Cwb	Td2	314 600	5.7
Equatorial	A	E	1 730 300	31.3
Rainforest, fully humid	Af	Eh1	48 400	0.9
Moonson	Am	Eh2	48 400	0.9
Savanna with dry summer	As	Ed1	181 500	3.3
Savanna with dry winter	Aw	Ed2	1 452 000	26.3

Climate codes used by Kottek *et al.* (2006) are included, but English-based codes were used in this paper. The total and percentage areas covered by each climate type in the study region are provided. Two poorly represented warm temperate climate subtypes were excluded from the table (and from analysis) but were included to compute total and percentage areas. Fully humid climates are those lacking a dry season with constant precipitation rates along the year. All calculations were based on grid cells in which the dominant climate subtype was assigned (see *Methods*).

species richness data are strongly spatially autocorrelated (see below and Appendix S2), which causes degrees of freedom and standard errors to be overestimated and underestimated, respectively (Legendre 1993; Diniz-Filho *et al.* 2003). To resolve this we calculated an autoregressive parameter (ρ) for each lineage within each climate type using pure autoregressive models in SAM 3.0 (Rangel *et al.* 2006) and then estimated the geographically effective sample size following the method described in Griffith (2003) based upon a single mean response.

Because climate types differed strongly in terms of area in the study region (Table 1; see also Appendix S1), we generated an area-based rank of the climate types and then calculated, for each species group, its Spearman rank-order correlation with the mean richness obtained when ignoring area. High positive correlations would indicate an effect of area on patterns of mean species richness among the climate types.

RESULTS

Patterns of species richness differed among older and recent groups, although there were some similarities, particularly in mountainous areas where richness tended to be high (Fig. 1). However, Pearson correlations of richness with elevation were positive and weak for gekkonids ($r = 0.142$), cordylids-scincids ($r = 0.239$), snakes ($r = 0.200$) and chameleons ($r = 0.547$) but negative for lacertids ($r = -0.286$). Gekkonids, lacertids and cordylids-scincids (the older groups) were richer in southern Africa, particularly in the west and along the Great Escarpment (Fig. 1a–c). Lacertids were absent from some eastern Africa areas (Fig. 1b) as were chameleons, which were also absent from parts of southern Africa (Fig. 1d). There were also few chameleons in southern Africa (Fig. 1d). Both chameleons and snakes (Fig. 1e) had high richness around Lake Victoria, and both groups were richest in the Albertine Rift Mountains. Snake richness was also high along the Great Escarpment. In general, the richness of all five groups had patterns of spatial autocorrelation characteristic of clines, with positive autocorrelations at shorter distances and most negative autocorrelations at larger distances (for details see Appendix S2).

Mean richness calculated for each Köppen–Geiger climate type (Fig. 2; for details see Appendix S4) indicated that the lineages were distributed differentially across current climate types. Gekkonids had higher mean richness in arid climates, and intermediate richness in temperate climates (Fig. 2a), with corrected 95% confidence intervals showing no overlap between the most arid climates (Ad1 and Ad2) and the most humid equatorial climates (Eh1 and Eh2). Similarly, for lacertids, higher and intermediate mean richness occurred in arid and temperate climates, respectively (Fig. 2b), but only the two most arid desert climates (Ad1, Ad2) significantly differed from every equatorial climate. Overall, these results indicated an association with arid conditions, and a secondary association with temperate climates for both gekkonids and lacertids. In contrast, cordylids-scincids were associated with temperate conditions (Fig. 2c). Even though this group was secondarily associated with arid climates, mean richness in these environments only differed significantly from equatorial savannas with dry winters (Ed2). Notably, associations with equatorial climates were weakest in gekkonids, lacertids and cordylids-scincids.

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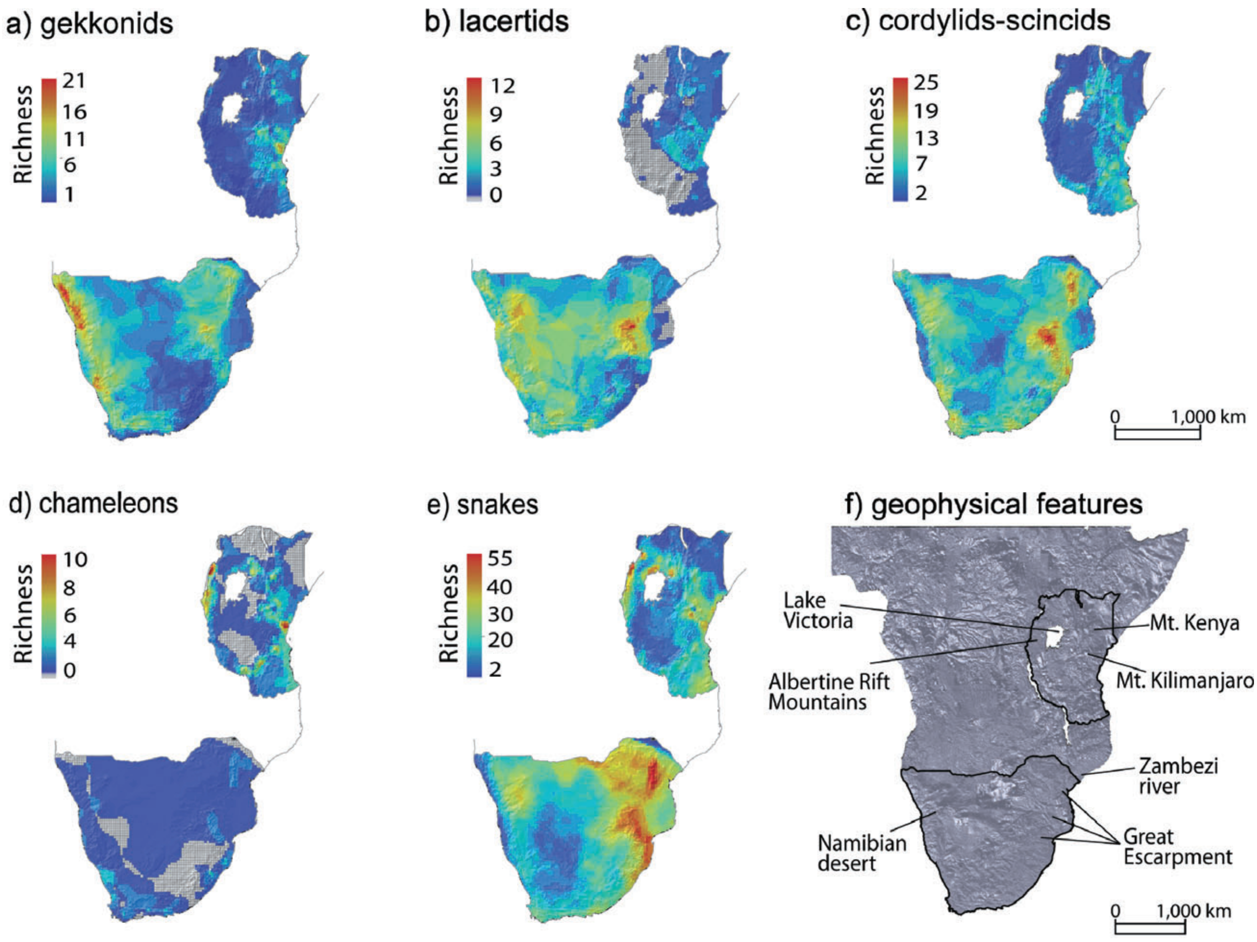

Fig. 1. Species richness patterns of five squamate reptile groups in eastern and southern Africa (a–e) at a 27.5-km scale. (f) Major geophysical features of Africa.

The climatic associations of chameleons and snakes (the more recent groups) were characterized by higher mean richness in equatorial climates and intermediate values in temperate ones, with no significant differences between both types of climates according to the 95% confidence intervals (Fig. 2d,e). For chameleons (Fig. 2d), mean richness in three equatorial climates (Eh1, Ed1 and Ed2) was significantly higher than in hot arid desert (Ad2) and in the two arid steppe climates (As1 and As2). For snakes, mean species richness was significantly higher in humid equatorial climates (Eh1 and Eh2) than in arid desert climates (Ad1 and Ad2). So, in contrast to the three older groups, chameleons and snakes showed a tendency to be preferentially associated with humid equatorial climates, while avoiding arid conditions.

Spearman rank-order correlations of mean richness against Köppen–Geiger climate type areas to test the influence of area on mean richness patterns were positive but not significant for gekkonids and cordylids-scincids ($r = 0.309$, $P = 0.328$; and $r = 0.049$, $P = 0.879$, respectively), positive and significant for lacertids ($r = 0.622$, $P = 0.031$), and negative and significant for chameleons and snakes ($r = -0.727$, $P = 0.007$; $r = -0.654$, $P = 0.021$, respectively). Thus, a potential effect of area on the mean richness patterns can be rejected for all groups except for lacertids.

DISCUSSION

The different groups of squamate reptiles had dissimilar distributions of species across current climate types. The key question is: do these distributions reflect characteristics prevailing in the palaeoclimates in which each group originated and/or radiated? To address this, we used the divergence times estimated by recent molecular phylogenetic hypotheses (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009) and reviewed the literature on palaeoclimates and fossil records to try to document when, where and under which environmental characteristics each group

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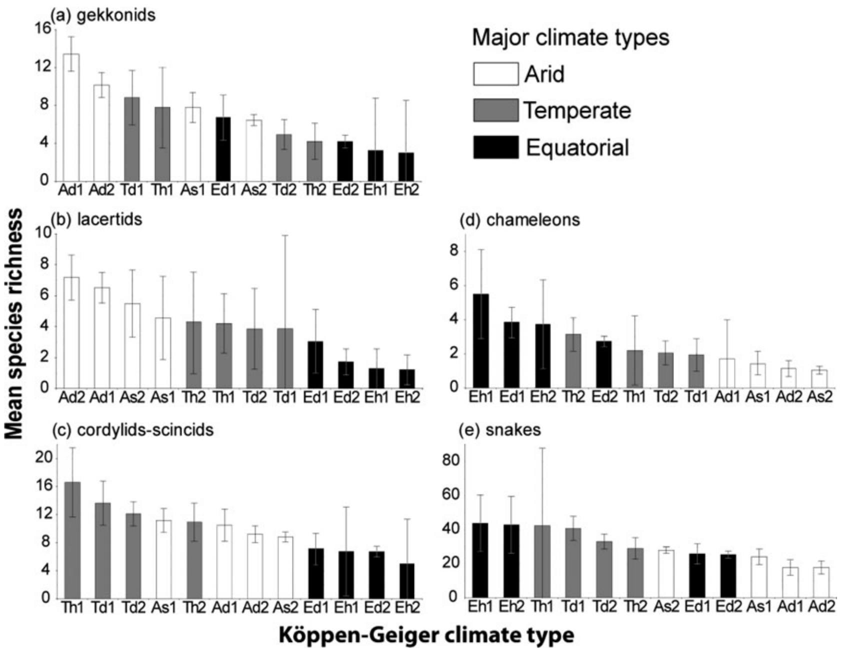

Fig. 2. Mean (±95% confidence intervals) species richness of five squamate reptile groups in the 12 Köppen–Geiger climate types occurring in southern and eastern Africa (see Table 1 for climate codes). Major climate types are differentiated with a white to black scale. Confidence intervals were calculated taken into account geographically effective degrees of freedom (see *Methods*).

might have arisen and evolved. We assumed that similarities between species richness patterns across climate types and the characteristics of the palaeoclimates in which the groups might have evolved indicate an influence of ancestral niches on contemporary species richness patterns (see Wiens & Donoghue 2004; Wiens & Graham 2005).

The divergence of gekkonids, cordylids-scincids and lacertids occurred during the Jurassic (about 196–145 Myr ago). According to palaeoclimatic reconstructions (Scotese *et al.* 1999; Rees *et al.* 2000; Ziegler *et al.* 2003), this period was predominantly arid in both the African portion of Gondwana (>80% of this area; see Table 1, Fig. 3) and across the planet (49%; see Table 1). The African Jurassic fossil record does not contain every lineage that diverged then. However, an African origin of cordylids has been suggested by Estes (1983), despite the lack of fossils in the early squamate fossil record of Gondwana (Evans 2003; Krause *et al.* 2003). A cosmopolitan distribution of early squamates across Gondwana has been proposed (Sampson *et al.* 1998) and is supported by several fossils (e.g. paramacellodid scincomorphs in Tanzania (Broschinski 1999); fragmentary reptile remains in Tanzania (Zils *et al.* 1995) and in India (Evans *et al.* 2002); remains of an early Jurassic lizard in South Africa (Kitching & Raath 1984); and squamate ancestors in the Karoo Basin of South Africa (Durand 2005; Rubidge 2005). So, if an African origin is accepted for gekkonids, cordylids-scincids and lacertids, they would have arisen during an arid Jurassic period deficient in warm humid (i.e. equatorial) conditions. The current distribution of the species of these groups indicates a propensity for arid and/or temperate climates in terms of species richness, with few species in equatorial climates. This is consistent with the hypothesis that niche conservatism has strongly influenced the richness gradients of these old groups.

For chameleons and snakes, the phylogenetic hypotheses (Kumazawa 2007; Vidal & Hedges 2009; Vidal *et al.* 2009) place the divergence of alethinophidian snakes and chameleons throughout the Cretaceous (about 145–65 Myr ago). During that period, arid climates contracted, and equatorial climates greatly expanded, covering a third of the African continent (Table 2, Fig. 3). Also, some simulations of Cretaceous palaeovegetation predict the existence of tropical rainforest in west-central Africa, tropical semi-deciduous forest in central Africa, and subtropical broad-leaved evergreen forests and woodlands in eastern and southern Africa (see Upchurch *et al.* 1998, their figure 2). Notably, the origin of chameleons has been placed in the Cretaceous in either eastern Africa or Madagascar (Hillenius 1959, 1986; Raxworthy *et al.* 2002); that is, coinciding with the areas that Upchurch *et al.* (1998) predicted to be occupied by tropical and subtropical forests. Along with this, several African snake fossils have been found in Cretaceous deposits (see Durand 2005) in Algeria (Rage

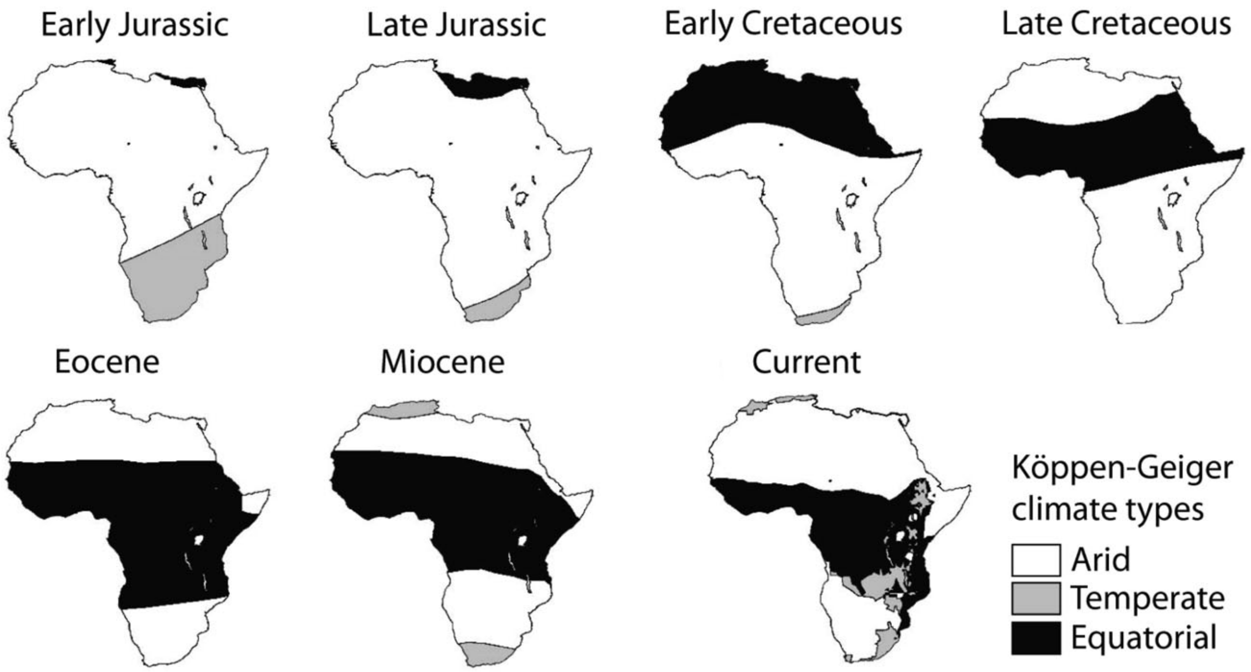

Fig. 3. The distribution of arid, equatorial and temperate Köppen–Geiger climates in relevant geological time periods for squamate reptile evolution in Africa. To facilitate comparisons among periods, the distribution of Paleoclimates (from Scotese 2002) has been adapted to the current shape of the African continent. The distribution of current climates is from Kottek *et al.* (2006).

Table 2. Major reptile radiation events (Rieppel *et al.* 1992; Evans *et al.* 2002; Raxworthy *et al.* 2002; Kumazawa 2007; Vidal & Hedges 2009) and their associated main Köppen–Geiger climate characteristics globally and in Africa as described in Scotese *et al.* (1999) and Scotese (2002)

				Köppen–Geiger climate area (%)		
Evolutionary event	Period	Myr ago	Region	Arid	Temperate	Equatorial
Divergence of gekkonids, cordylids-scincids and lacertids	Early–late Jurassic	199–145	Global	27.3–48.7	41.3–35.1	26.3–7.2
			Africa	80.9–92.6	17.9–3.3	1.0–4.1
Divergence of chameleons and snakes	Early–late Cretaceous	145–65	Global	32.2–28.2	28.7–38.9	23.3–20.4
			Africa	61.6–62.8	1.3–0	37.0–37.2
Major radiation of chameleons and snakes	Eocene–Miocene	55–18	Global	21.3–25.8	39.4–22.0	33.7–26.8
			Africa	39.4–41.3	0–4.9	60.6–53.7
Current	Present	0	Global	24.7	61.4	13.9
			Africa	54.8	13.9	31.3

All calculations considered two Köppen–Geiger major climate types (i.e. snow and polar), which were excluded from the table as they did not occur in Africa. Palaeoclimate reconstructions by Upchurch *et al.* (1998), Rees *et al.* (2000) and Ziegler *et al.* (2003) were also reviewed and found to be consistent in general with these data.

& Escuillié 2003), Morocco, Lybia and Egypt (Nessov *et al.* 1998; Rage & Cappetta 2002) and Sudan (Rage & Werner 1999). Those sites are believed to have had tropical climates at that time (Scotese *et al.* 1999). We found that, on average, the species richness of chameleons and snakes is currently lower in arid climates, and higher in equatorial and temperate climates. Accepting the imprecise nature of palaeoclimatic reconstructions and uncertainties in identifying where and when major clades arose, the predominately equatorial characteristics of the areas in which each of these groups may have originated (see above) suggests that niche conservatism also influences the contemporary distribution of chameleons and snakes.

The Eocene-Miocene (about 55–18 Myr ago) represents another key period, as major radiations within vertebrate taxa during this time gave rise to many of the extant vertebrate groups (Clarke & Crame 2003; Vermeij 1987), including the chameleons and snakes (Kumazawa 2007; Sanders & Lee 2008; Vidal &

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Hedges 2009; Vidal *et al.* 2009). This followed the Paleocene-Eocene thermal maximum and has been characterized by higher homogeneity of global temperatures and by the presence of equatorial rainforest as far as 45° North (Zachos *et al.* 2001). In Africa, equatorial climates occupied more than half of the continent, and arid climates more than one-third at the end of the period (Cerling *et al.* 1997) (Fig. 3). The African reptile fossil record during the Eocene-Miocene includes every lineage considered in this study (e.g. Pickford *et al.* 1996; Rage 2003). In particular, all records of chameleons and most records of snakes were in Kenya, Tanzania and Uganda (e.g. Pickford & Andrews 1981; Pickford *et al.* 1986; Rieppel *et al.* 1992), which were likely within the equatorial realm during the Eocene-Miocene (Fig. 3). Hence, the proliferation of species of chameleons and snakes would have occurred within equatorial climates, which is again consistent with the observed current patterns for equatorial and arid climates shown by both groups. This also identifies niche conservatism as a potential influence on the current distribution of the richness patterns of both groups.

Finally, it should be noted that the most humid Köppen–Geiger equatorial climates – rainforest, fully humid (Eh1) and Moonson (Eh2) climate types – are poorly represented in our study region, where they only cover 1.8% of the area. Both climate types contained the fewest species of the three older groups (gekkonids, lacertids and cordylids-scincids), but contained the richest assemblages of the more recent groups (chameleons and snakes) (see Fig. 2). The limited representation of equatorial climates in the study area may influence the power of statistical analyses, which found only a few cases of significant differences in mean species richness between climate types. Thus, it is possible that an extended database encompassing all of central Africa and its large equatorial band would render clearer positive and negative associations of the recent and older groups for these climates.

In sum, although exploratory analyses such as this one cannot be considered formal tests of explanations for biogeographical patterns (as discussed by Kerr *et al.* 2007), our data contain historical signals in the contemporary species richness gradients of African squamates that can be interpreted as the result of niche conservatism. Gaps of knowledge in the fossil record, and uncertainties regarding both the characteristics of past climates and the phylogenetic relationships among squamate groups (which are themselves hypotheses to be tested), require some caveats with respect to our interpretations of the patterns. Even so, until these gaps are filled, our results contribute to the growing evidence that niche conservatism strongly influences current species richness gradients.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Current distribution of Köppen–Geiger climates within the study area.

Appendix S2. Moran's *I* spatial correlograms for the species richness variation of five reptile groups.

Appendix S3. Richness maps at the 110 × 110 km. grid showing the 456 cells used for analysis of gekkonids (a), lacertids (b), cordylids-scincids (c), chameleons (d) and snakes (e). Panel (f) shows the 110 km analysis overlaying the map of Kottek *et al.*'s (2006) climatic regions.

Appendix S4. More detailed representation of Figure 2.

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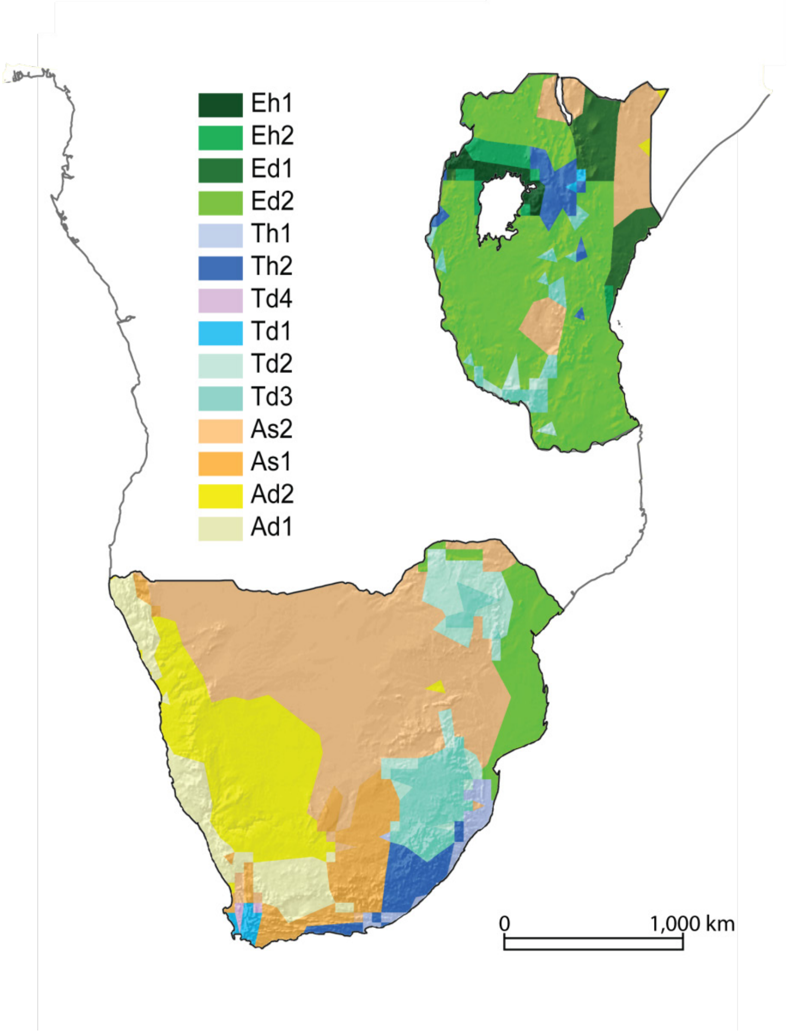
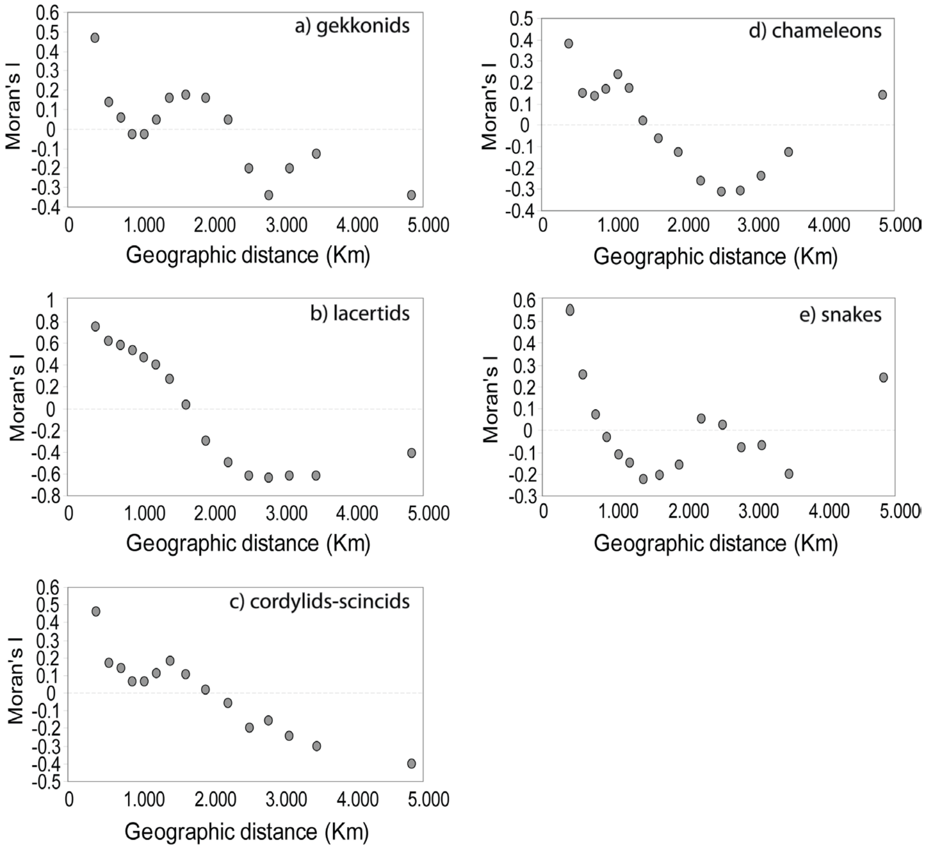
Appendix S1

Current distribution of Köppen-Geiger climates within the study area (extracted from Kottek 2006). Eh1: Equatorial rainforest, fully humid; Eh2: Equatorial monsoon; Ed1: Equatorial savannah with dry summer; Ed2: Equatorial savannah with dry winter; Ad1: Arid desert cold; Ad2: Arid desert hot; As1: Arid steppe cold; As2: Arid steppe hot; Th1: Warm temperate, fully humid hot; Th2: Warm temperate, fully humid warm; Td1: Warm temperate with dry summer, warm; Td2: Warm temperate with dry winter, hot; Td3: Warm temperate with dry winter, warm; and Td4: Warm temperate with dry summer, hot.



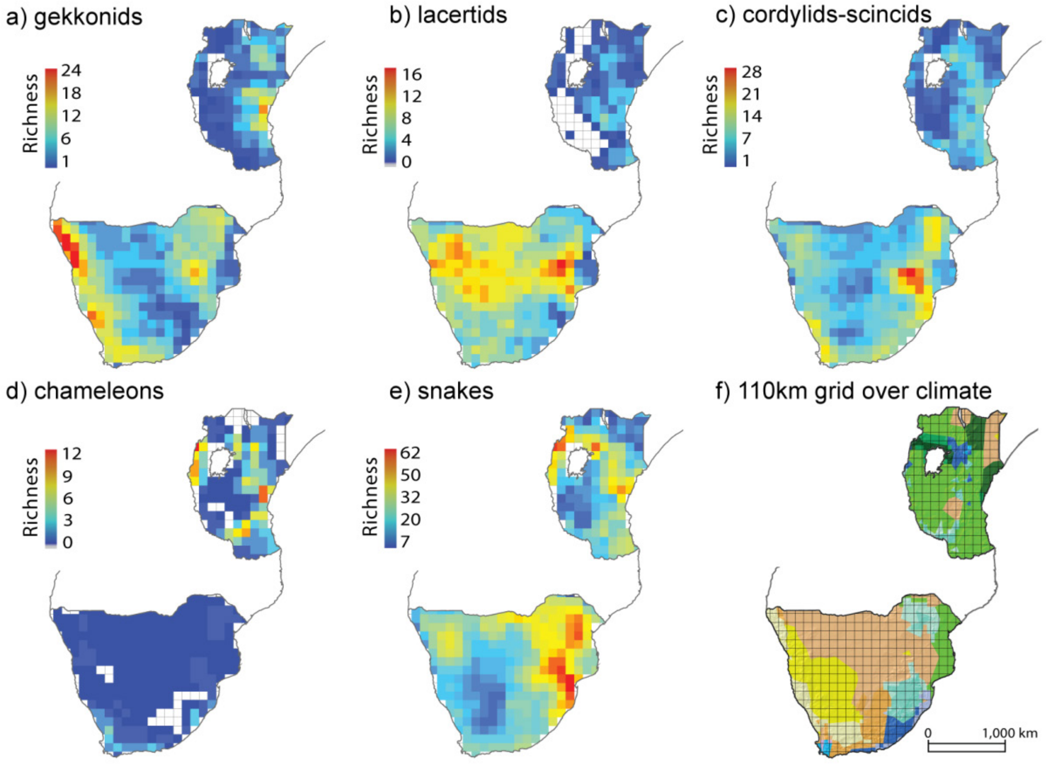
Appendix S2

Moran’s I spatial correlograms for the species richness variation of gekkonids (a), lacertids (b), cordylids-scincids (c), chameleons(d) and snakes (e), across southern and eastern Africa. The patterns of spatial autocorrelation are characteristic of clines for the five groups. Clinal variation was particularly clear for lacertids (b) which may be related to the distinctive negative correlation with altitude shown by the group (r = -0.286, see text). For the other groups (a, c-e) a secondary peak of positive autocorrelation occurred at low-intermediate to intermediate distances, reflecting the more patchy distribution of the high richness spots of these groups across the study area (see Fig. 1). All correlograms were built using SAM 3.0 (Rangel *et al.*, 2006) for 15 distance classes with upper limits ranging from 394 to 4.846 km.



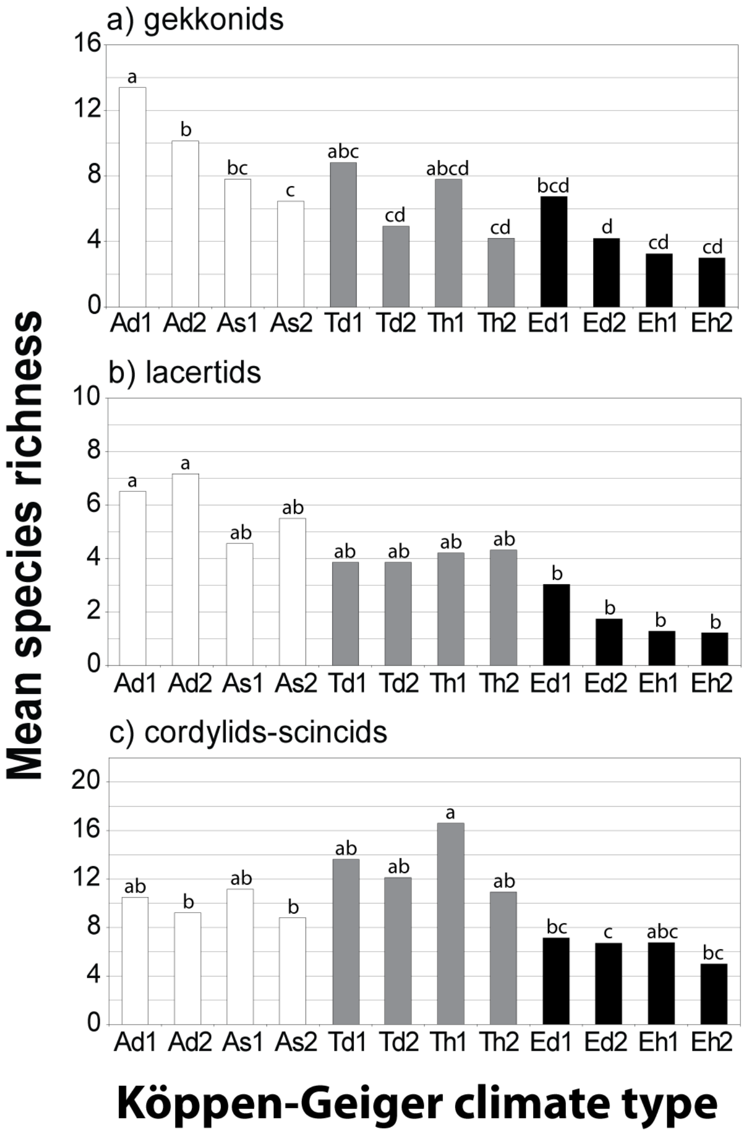
Appendix S3

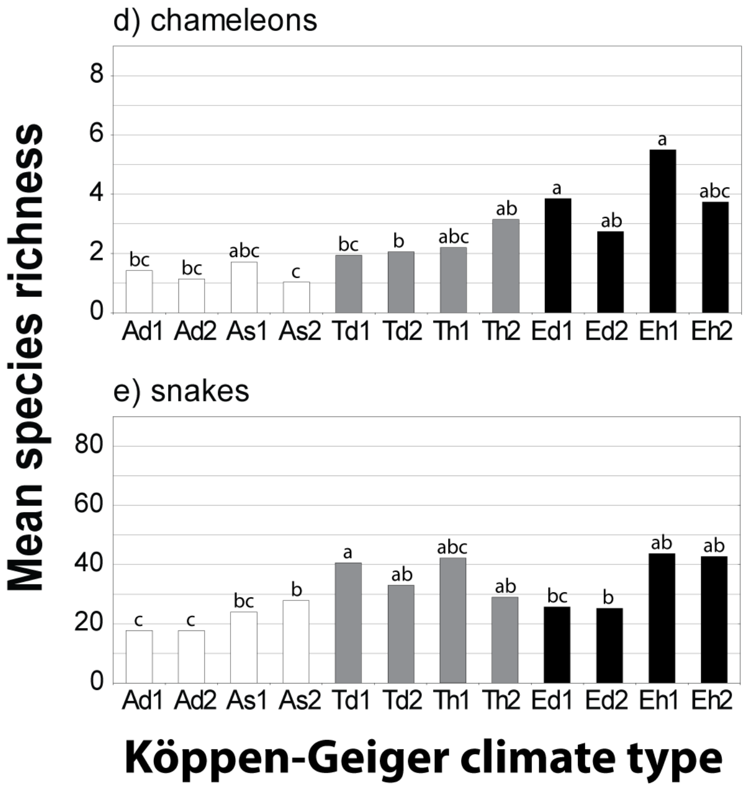
Richness maps at the 110 x 110 km. grid showing the 456 cells used for analysis of gekkonids (a), lacertids (b), cordylids-scincids (c), chameleons (d) and snakes (e). Panel (f) shows the 110 km analysis overlaying the map of Kottek's *et al.* (2007) climatic regions.



Appendix S4

Detailed representation of Figure 2. The augmented panels include letters derived from pairwise comparisons of climates for each group. Comparisons are made according to the overlap of the corrected 95% confidence intervals equivalent to a Least Significant Difference test. Climatic regions are equally ordered in every panel following a climatic gradient to facilitate comparison among groups. The confidence intervals are not included here to avoid redundancy in information.





d) chameleons

e) snakes

3. Phylogenetic relationships in New World Bird range size patterns

Bradford A. Hawkins, Ignacio Morales-Castilla, Ramnik Kaur & Miguel Á. Rodríguez.

Capítulo 3

Geografía de las señales filogenética y no-filogenética del tamaño de rango de paseriformes oscines (Aves) del Nuevo Mundo

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

HAWKINS, B. A., MORALES-CASTILLA, I., KAUR, R. and RODRÍGUEZ, M. Á. Geography of the phylogenetic and non-phylogenetic signals in range sizes of New World oscine passerines (Aves).

Resumen

Objetivo: Cuantificar el grado en que las relaciones filogenéticas condicionan el tamaño de los rangos geográficos de distribución total, reproductivo y no reproductivo de aves paseriformes oscines, y examinar la estructura espacial de las señales filogenéticas y no filogenéticas.

Localización: Hemisferio occidental.

Métodos: Los tamaños de rango geográfico fueron obtenidos para las 423 especies del Neártico y el Neotrópico incluidas en la filogenia de oscines; los rangos totales y reproductivos se estimaron para todas las especies y los rangos no reproductivos para 125 especies migratorias. Se utilizó la regresión de autovectores filogenéticos (PVR) para separar la variación del tamaño de rango en sus componentes filogenético y no-filogenético; componentes que posteriormente fueron mapeados para documentar sus patrones espaciales. Se utilizaron modelos de regresión para explorar relaciones entre patrones espaciales de tamaño de rango promedio con variables ambientales, o con la latitud en Norte América y longitud en Suramérica, esto último al objeto de estimar las contribuciones de los componentes filogenético y no-filogenético de los rangos de distribución a los gradientes espaciales.

Resultados: La señal filogenética explicó el 16.2% de la variación de los rangos no reproductivos, el 19.9% de los rangos reproductivos y el 24.2% de los rangos totales. Las contribuciones del componente filogenético a los patrones espaciales de los tamaños medios de rango fueron variables, comprendiendo desde el 12% de la variación de los rangos reproductivos en Norteamérica, al 49% de variación de los rangos no reproductivos en Sudamérica. El componente variable ambiental más correlacionado con el tamaño de rango fue la interacción entre temperatura media y el rango espacial de temperatura, una medida de gradientes climáticos de meso-escala. Esta interacción también fue el elemento ambiental más correlacionado con los componentes no filogenéticos de los rangos totales y reproductivos. Los modelos para los componentes filogenéticos fueron idiosincrásicos.

Principales conclusiones: El tamaño de rango de oscines contiene una señal filogenética baja a moderada que está espacialmente estructurada. Por tanto, la macroevolución contribuye a configurar los tamaños de rango a nivel de especie y de ensamblaje, sugiriendo una cierta estabilidad evolutiva de rasgos biológicos relacionados con los rangos de distribución (como el tamaño de cuerpo y la capacidad dispersora). Actualmente, es posible identificar factores ambientales que pueden explicar entre el 40-65% de la variación en los componentes filogenético y no filogenético de los patrones de tamaño de rango, pero aproximaciones basadas en otros rasgos biológicos serán necesarias para comprender las causas de la biogeografía del tamaño de rango.

Palabras clave: heredabilidad del tamaño de rango, conservación de nicho, Paseriformes oscines, regresión de autovectores filogenéticos, tamaño de rango, Regla de Rapoport.

Geography of the phylogenetic and non-phylogenetic signals in range sizes of New World oscine passerines (Aves)

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Abstract

Aim To quantify the extent to which phylogeny influences the sizes of total, breeding and non-breeding ranges of oscine passerines and examine the spatial structure of the phylogenetic and non-phylogenetic signals.

Location Western Hemisphere.

Methods We calculated range sizes for 423 Nearctic and Neotropical species included in an oscine supertree. Total and breeding range sizes were calculated for all species, and non-breeding ranges were calculated for 125 migratory species. Phylogenetic eigenvector regression (PVR) partitioned range sizes into phylogenetic and non-phylogenetic components, and all were mapped to document spatial patterns. Environment-based regression models explored correlates of the pattern of mean range sizes, and the range size metrics were regressed against latitude in North America and longitude in South America to isolate contributions of phylogenetic and non-phylogenetic components to spatial gradients.

Results Phylogenetic signal explained 16.2% of the variance in non-breeding, 19.9% in breeding, and 24.2% in total range sizes. Contributions of the phylogenetic components to the spatial patterns of mean range sizes were variable, ranging from 12% of the variance in breeding ranges in South America to 49% for non-breeding ranges in South America. The strongest environmental correlate of ranges sizes was the interaction between average temperature and spatial range in temperature, a measure of meso-scale climatic gradients. It was also the strongest correlate of the non-phylogenetic component of total and breeding ranges. Models for the phylogenetic components were idiosyncratic.

Main conclusions Oscine range sizes contain low to moderate phylogenetic signal that is spatially structured. Thus, macroevolution contributes to range sizes patterns at both the species and assemblage level, suggesting that associated traits are not entirely labile. It is currently possible to identify environmental factors that can account for 40-65% of the variance in phylogenetic and non-phylogenetic components of range size patterns, but trait based approaches will be necessary to evaluate fully the drivers of the biogeography of range size.

Keywords: heritability of range size, niche conservatism, oscine passerines, Passeriformes, phylogenetic eigenvector regression, range size, Rapoport's Rule

Introduction

The extent to which macroevolution contributes to the sizes of species' geographic ranges is not well resolved. Following a report of substantial species-level heritability of range size in extinct marine mollusks (Jablonski, 1987), attempts to measure phylogenetic signal in range sizes among extant terrestrial species found little or none (Gaston, 1998; Webb & Gaston, 2003; Webb & Gaston, 2005, and references therein). On the other hand, range sizes undoubtedly reflect species traits to some extent, many of which are strongly conserved during cladogenesis (Freckleton *et al.* 2002), so it would be surprising if there were no phylogenetic signal in range sizes at all (see, e.g., Pocock *et al.* [2006], Bocxlaer *et al.* [2010] and Buckley [2010]). A summary of 16 data sets by Waldron (2007) reported statistically significant phylogenetic structure in range sizes in 11. Of five analyses of various bird clades, three reported heritability at some level.

An aspect of phylogenetic signal in range sizes that has received no attention is whether or not the signal, when it occurs, contains spatial structure. Range size represents one of the major 'traits' of species on which macroecologists have focused, and there is an extensive literature on Rapoport's Rule, which states that range sizes are larger in cold, extra-tropical climates than in tropical climates. Where and under what conditions Rapoport's Rule applies has been the subject of many papers and much debate, as has the issue of whether it is better studied using an explicit geographic framework or than the individual species focus (Ruggiero & Hawkins, 2006). Part of the problem with using geographically focused approaches has been that although a number of comparative methods have been devised to incorporate phylogenetic information into species-level studies, spatially explicit methods are less well known (Kidd & Ritchie, 2006). However, the development of phylogenetic eigenvector regression (PVR, Diniz-Filho *et al.*, 1998; Desdevises *et al.*, 2003) has led to geographically explicit macroecological analyses in a phylogenetic context, allowing patterns to be partitioned into phylogenetically structured and non-phylogenetic components (Diniz-Filho *et al.*, 2007, 2009; Ramirez *et al.* 2008; Terribile *et al.*, 2009). This allows us to both 'control' for phylogeny when examining geographical patterns and to quantify the extent to which phylogenetic inertia contributes to observed gradients.

In this paper we quantify the level of phylogenetic signal in range sizes for a subset of oscine passerines included in a global species-level supertree (Jønsson & Fjeldså, 2006). Based on the literature we expected a somewhat weak signal at the species level. However, we also explore two aspects of the heritability of bird range sizes that have never been examined. First, we document the geographical pattern of phylogenetic and non-phylogenetic structure of range sizes across two continents. Second, birds represent a somewhat unusual group for studying range dynamics, because many species are migratory and have distinct breeding and non-breeding ranges, often thousands of kilometers apart. The environmental influences on these parts of the range could be substantially different, as could levels of phylogenetic conservatism of traits that influence range sizes in summer and winter. Because non-breeding ranges are not well known in all parts of the world, we focus on New World species, for which exist widely used digitized distribution maps in both the breeding and non-breeding seasons (Ridgley *et al.*, 2007). The geographic pattern of breeding range sizes of New World birds has already been documented, and environmental models of mean range sizes across the continents have identified potential climatic and habitat drivers (Hawkins & Diniz-Filho, 2006). But as in all macroecological studies that do not include explicit phylogenetic information, it is not possible to evaluate the extent to which gradients reflect adaptive responses to environmental conditions independent of phylogenetic history as opposed to patterns whose origins lie in evolutionary time and reflect conservatism of traits during cladogenesis. Currently, the absence of a supertree for all groups precludes an analysis of all birds.

Material and Methods

Bird data

Breeding and non-breeding ranges of all native oscines were extracted from the database available at http://www.natureserve.org/getData/birdMaps.jsp, downloaded in November, 2009. Island endemics and species whose ranges extend beyond the Western Hemisphere were deleted from the dataset. The remaining 1110 species were compared against the species included in the supertree of Jønsson & Fjeldså, (2006), and the 423 species in the tree for which we had matching range maps were extracted for analysis. The phylogeny was then rebuilt, including only the species used in the PVRs.

Three range sizes were quantified: breeding, non-breeding, and total (the sum of breeding and non-breeding ranges) (see Appendix S1). Although island endemics were excluded, island distributions of species also occurring on the mainland were included in range size calculations, but passage ranges were not. The data were binned in a 9,319 km2 grid in a Behrmann projection (ca. 96.5 x 96.5 km at the equator), and mean geometric range sizes were calculated for each cell.

We also generated richness maps for the oscines based on breeding, non-breeding and total ranges. Richness patterns for all New World birds based on breeding ranges have been documented (Hawkins *et al.*, 2006), but as far as we know richness patterns for any groups of migratory species in their winter ranges have never been mapped. Although our data set does not include all species of oscines, the richness patterns should be representative and were used to facilitate interpretation of the range size patterns.

Phylogenetic eigenvector regression

PVR was used to partition range sizes into phylogenetically autocorrelated (PA) and phylogenetically independent (PI) components. The PI component is sometimes referrred to as the adaptive component, but it can be interpreted in more complex ways (Desdevises *et al.*, 2003). Here we simply distinguish the part of range size correlated with phylogeny and the part evolving independently. This method is one among a variety of phylogenetic comparative methods that are used to determine how phylogenetic relationships influence comparative analyses. Of the methods available, PVR has an advantage of not requiring a particular evolutionary model (see Diniz-Filho and Tôrres, 2002). It is also very easy to map the outputs. The method has been criticised (Rohlf, 2001, see below), and the issues raised have been considered in our analysis.

In PVR a trait (e.g., range size) is regressed against a set of phylogenetic eigenvectors that describe the phylogenetic relationships among the species in a clade. The phylogeny is first converted into a pairwise phylogenetic distance matrix, in our case based on the numbers of nodes separating species, and then transformed into phylogenetic eigenvectors through a Principal Coordinates Analysis. The selection of the specific eigenvectors to be included in the PVR is a critical issue because both the number of eigenvectors and the existence of phylogenetic autocorrelation in the residuals can affect the results. We used the algorithm proposed by Griffith and Peres-Neto (2006), implemented in Matlab 7, to select the smallest set of eigenvectors needed to reduce all phylogenetic autocorrelation in the residuals of the PVR to non-signficant levels (see Appendix S2) ; these residuals are interpreted as the component of range size independent of phylogenetic structure (PI). The phylogenetic (PA) component is represented by the range sizes predicted from the phylogenetic relationships among the species.

The eigenvector approach can introduce bias in the estimation of the PA component of range sizes (or any other trait), since inclusion in the PVR of 422 vectors based on the phylogeny of 423 species would explain all of the variance in the data (Rohlf, 2001). To test the observed phylogenetic signals against those expected when using eigenvectors, we compared the PA components against null models generated by taking 1000 random samples of the log-transformed range sizes without replacement and regressing them against the set of vectors included in the PVRs. Estimated PA’s>0 represent the potential bias introduced by the selected eigenvectors. Experience with the method has also indicated that the null value of PA in a PVR (i.e., the null R^2) can be closely estimated by dividing the number of eigenvectors in the regression by the number of taxa. A total of nine range size metrics were generated: observed total ranges and their PA and PI components, observed breeding ranges and their PA and PI components, and observed non-breeding ranges (for migratory species only) and their PA and PI components.

Finally, following Ramirez *et al.* (2008), we estimated the proportions of the spatial pattern in the observed range sizes attributable to phylogenic and non-phylogenetic responses. This was done by first regressing the mean range size in each cell (total, breeding or non-breeding) against the dominant spatial axis (latitude north of 12°N and longitude south of 12°N) to estimate the slope of each range size gradient. We then regressed both the mean PA-component of each range metric and the difference between the observed and phylogenetic mean range size (the average PI-component) against latitude or longitude. Because the sum of the slopes of the phylogenetic and non-phylogenetic components of each gradient is equal to the slope of the total observed gradient, the proportional contribution of each component can be estimated by dividing the component slopes by the total slopes. We also correlated the observed vs. the phylogenetic and non-phylogenetic components of each range size metric in the north and south to evaluate overall levels of covariation.

Environmental correlates of mean range size

Environmental infuences on mean range sizes were generated using Ordinary Least Squares simple and multiple re-gression comprising seven spatially structured variables. The primary focus was on three variables expected to be associated with bird distributions: (1) continental width, measured as the dis-tance from the west to east coasts for each row of cells, included because spe-cies can more easily spread longitudinal-ly than latitudinally and may be con-strained by availability of land (Rapoport, 1982), (2) the product of annual temperature (+16°C to make all values positive) x the range in temperature within the cell, measured by the difference between highest and lowest temperatures using the 30 arc-second BIO1 database in Worldclim, v. 1.4, http://www.worldclim.org), included because of a known association between meso-scale temperature gradients and range sizes of New World birds (Hawkins & Diniz-Filho, 2006), and (3) mean annual temperature (extracted from BIO1), included because it is considered by some an important environmental driver of Rapoport's Rule (Stevens, 1989). Also included as predictors were the standard deviation in elevation within cells using all pixils (calculated from a 30 arc-second digital elevation model), net primary productivity (http://sedac.cisin.columbia.edu/es/hanpp.html#data), the global vegetation index (http://www.ncdc.noaa.gov/oa/podguide/ncdc/docs/gviug/ index.htm), and annual actual evapotranspiration (http://www.grid.unep.ch/data/ download/gnv183.zip). Our goal was not to generate complex and detailed models of range sizes, but to evaluate the extent to which a set of potential environmental predictors were able to describe the spatial patterns in the data. With one exception (see Results), the first three variables were the strongest correlates of the nine range size metrics.

Results

Richness gradients

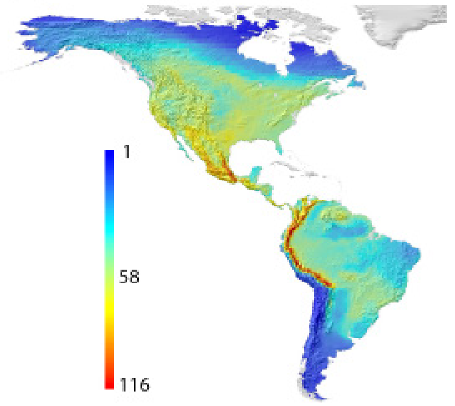
The richness patterns for the subset of oscines obtained by the combination of breeding and non-breeding distributions (Fig. 1a) and during the breeding season only (Fig. 1b) shows a pattern similar to that seen for the richness gradient of a partially overlapping group of families by Hawkins *et al.* (2006) ('derived' families). Maximum richness occurs in the tropical Andes and mountain ranges of tropical Mexico across the entire year, and in the tropical Andes during the North American winter. Richness is not particularly high in the lowland tropics, and richness is higher in parts of temperate North America than in the Amazon Basin. The loss of large number of species in the southeastern USA in winter coupled with the increase in the number of species in central and southern Mexico apparent when comparing year-round richness against breeding season richness reflects the fact that most migrating oscines overwinter in Mexico (Fig. 1c), with a moderate number of Canadian species settling in the southern USA. A few species in the data set migrate as far south as South America.

Range size gradients

Combining breeding and non-breeding ranges generates a geographic gradient reflective of Rapoport's Rule in North America (Fig. 2a), with broad ranges on average across most of Canada (except in northeastern Nunavut), moderate ranges in the eastern USA, and narrow ranges in the southwestern USA southward. Patterns in South

America differ substantially (Fig. 2a), with broad average ranges in northeastern Brazil and the narrowest ranges in the Andes. Patterns for breeding ranges are qualitatively similar (Fig. 2b), with Rapoport's Rule holding over most of North America but the converse in lowland South America and a very strong effect of the Andes. Range size patterns among migratory species are also similar, except that the few species that migrate to the Andes during the Northern Hemisphere winter have moderate to large non-breeding ranges (Fig. 2c). Overall, all combinations of ranges show a similar pattern, Rapoport's Rule in North America and its converse in South America.

(a) Total ranges (all spp.)



(b) Breeding ranges (all spp.)

(c) Nonbreeding ranges (migratory spp.)

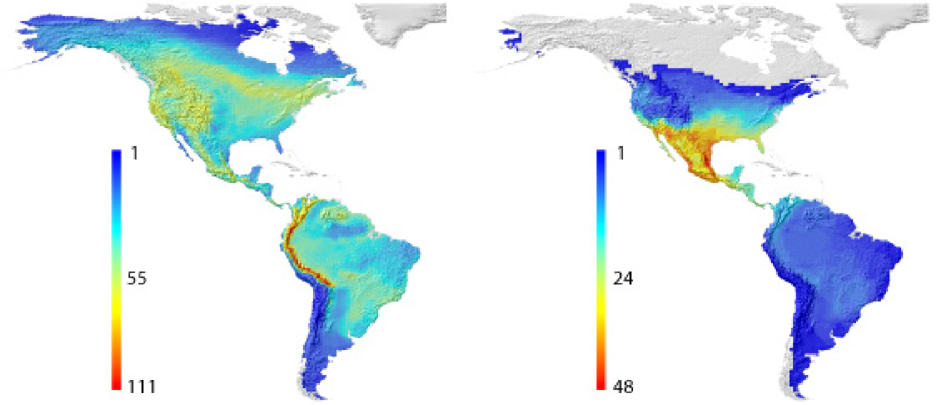
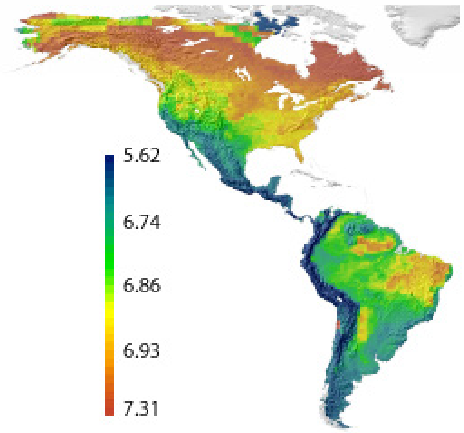
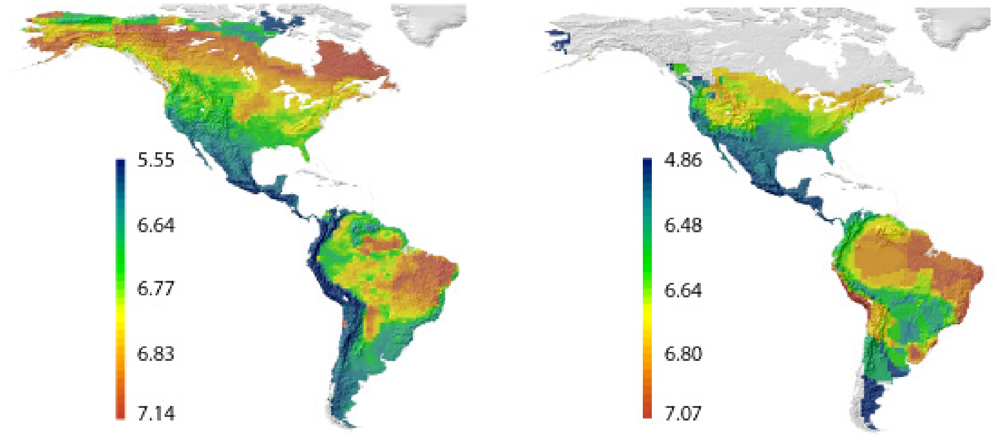


Fig. 1. Species richness gradients for the species of oscine passerines in the data set based on three range size metrics. (a) Richness summed over the year by combining breeding and non-breeding ranges (S = 423), (b) richness during breeding season only (S = 423), and (c) richness of migratory species while in their non-breeding ranges (S = 125).

(a) Mean log total range size





(b) Mean log breeding ranges size

(c) Mean log nonbreeding range size

Fig. 2. Mean range sizes of (a) breeding and non-breeding ranges combined, (2) breeding ranges only, and (3) non-breeding ranges of migratory species only.

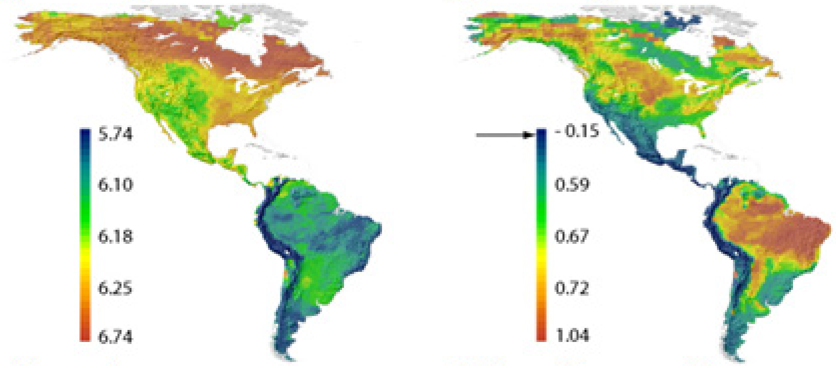
Partitioning phylogenetic and non-phylogenetic components of range size

The PVRs identified significant phylogenetic signal in all three range size metrics (total ranges R^2 = 0.242; breeding ranges R^2 = 0.199, and non-breeding ranges R^2 = 0.162). All estimates of P were greater than expected under random models (13 eigenvectors generating a total range mean R^2 = 0.033, SE = 0.001; 10 eigenvectors generating a breeding range mean $R^2 = 0.028$, SE = 0.001; 8 eigenvectors generating a non-breeding range mean $R^2 = 0.066$, SE = 003). Thus, a maximum of one-quarter of the range sizes of these 423 passerines can be accounted for by their phylogenetic relationships.

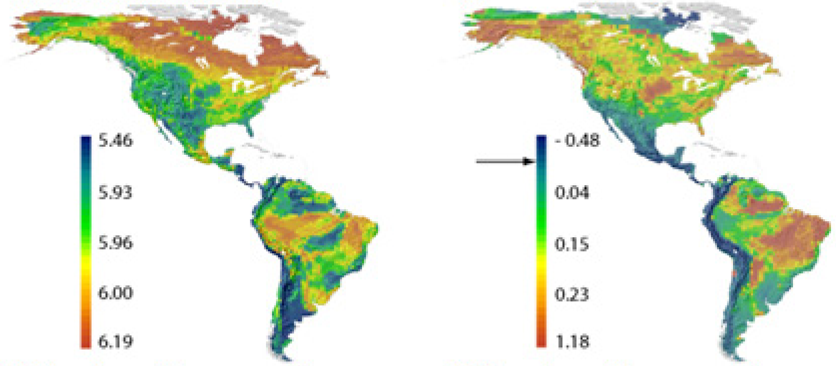
Based on the phylogenetic relationships among the species, average total (breeding + non-breeding) range sizes in North America are predicted by the PVR be to substantially larger than in South America (Fig. 3a). The non-phylogenetic (residual) signal, in contrast, comprises somewhat patchily distributed large ranges in the USA and Canada, with strong positive non-phylogenetic responses in the lowland tropics of South America (Fig. 3b). Phylogenetic structure also generates the expectation that breeding ranges should be largest in central and eastern Canada, but unlike total ranges also in parts of tropical and subtropical South America (Fig. 3c). The non-phylogenetic component has a similar structure, except in northern Nunavut (Fib. 3d). Non-breeding ranges are predicted by phylogeny to be largest in tropical South America (Fig. 3e), although this is based on relatively few species (see Fig. 1c). Those species that overwinter in North America have much larger ranges to the north than to the south than expected by their phylogenetic relationships (Fig. 3f). The non-phylogenetic pattern in South America appears patchy, but again this is based on few species.

Partitioning the slopes of observed spatial patterns of range sizes into the contributions of phylogenetic and non-phylogenetic components indicates that in five of the six data sets, the non-phylogenetic component accounts for two-thirds to over 90% of the observed gradients (Table 1). Non-breeding ranges in South America, on the other hand, show more balanced contributions of both components. The importance of non-phylogenetically structured responses to observed gradients is further indicated by the much stronger correlations between observed and non-phylogenetic mean range sizes than found for mean range sizes predicted by phylogeny, again with the exception of non-breeding ranges in South America (Table 1).

(a)Total range PA (b)Total range PI



(c)Breeding range PA (d)Breeding range PI



(e)Non-breeding range PA (f)Non-breeding range PI

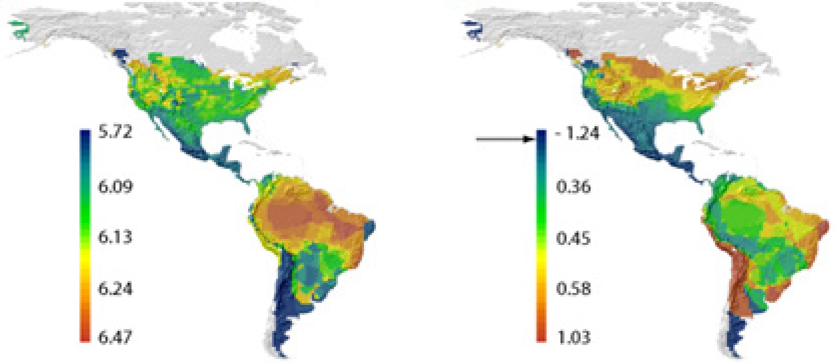


Fig. 3. Spatial pattern of the phylogenetic (PA) and phylogenetically independent (PI) components of mean range size for total ranges (a, b), breeding ranges (c, d) and non-breeding ranges (e, f). The arrows in the colour scales of the non-phylogenetic components are cells in which ranges are the size expected based on phylogeny (i.e., birds in these cells show no non-phylogenetic response on average). Negative values reflect that ranges are smaller than expected, and positive values reflect that ranges are larger than expected.

Environmental correlates of mean range sizes

The explanatory power of saturated multiple regression models including all seven predictors ranged from moderate to good, except for the non-phylogenetic component of non-breeding ranges (Table 2). In most models a single predictor accounted for most of the explained variance. All observed range metrics were best explained by average temperature x range in temperature, indicating that the narrowest ranges are found in tropical mountains (warm macroclimates with strong elevational temperature gradients), although the relationship was weaker for non-breeding ranges (see Fig. 2).

Table 1. Slopes of regressions of mean total, breeding and non-breeding range sizes against latitude (NORTH of 12°N) and longitude (SOUTH of 12°N) with partial slopes of phylogenetic (PA) and non-phylogenetic (PI) components. The percentages (%) reflect the relative contribution of each component to the observed gradient. Coefficients (r) provide the correlation between each component and the observed mean range sizes.

Range metric	Observ. slope	PA slope (%)	PI slope (%)
NORTH			
Total range	0.007	0.0025 (36%) (r = 0.656)	0.0045 (64%) (r = 0.908)
Breeding range	0.0074	0.0023 (31%) (r = 0.338)	0.0051 (69%) (r = 0.950)
Non-breeding range	0.0118	0.0021 (18%) (r = 0.362)	0.0097 (82%) (r = 0.972)
SOUTH			
Total range	0.0121	0.0009 (7%) (r = 0.676)	0.0112 (93%) (r = 0.973)
Breeding range	0.0145	0.0017 (12%) (r = 0.372)	0.0128 (88%) (r = 0.976)
Non-breeding range	0.0095	0.0047 (49%) (r = 0.718)	0.0048 (51%) (r = 0.750)

The strongest correlates of the phylogenetic components were more idiosyncratic (Table 2), reflecting the differences in their spatial patterns (Fig. 3a,c,e). The single strongest trend in the phylogenetic component of breeding ranges was continental width (see Fig. 3c), but the relationship was weak (Table 2). Net primary productivity was a moderately strong predictor of the PA-component of the relatively few species that overwinter in South America, reflecting the large non-breeding ranges of those species in tropical forest and northern cerrado (Fig. 3e).

Table 2. Environmentally based regression models for the observed, phylogenetic components and non-phylogenetic components of mean total oscine range size, mean breeding range size and mean non-breeding range size. The simple regression r2 identifies the single strongest predictor of range size and its coefficient of determination, and the multiple regression R^2 represents the variance explained by a saturated model including seven environmental variables. The saturated models can be interpreted as the total proportion of variance in spatial structure that can be explained by the available spatially patterned environmental predictors, and the simple regressions identify the contribution of the single strongest predictor. Variable codes are: Temp = mean annual temperature, Width = the distance from the west to east coasts for each row of cells, NPP = net primary productivity, and TxR = the product of mean annual temperature (+16°Cº) and the range of temperatures in the cell (a measure of the interaction of macroclimate and temperature gradients within cells).

Range metric	Simple regression r^2	Multiple regression R^2
Total range (breeding + non-breeding)		
Observed	TxR = 0.545	0.651
PA	Temp = 0.453	0.627
PI	TxR = 0.451	0.593
Breeding range		
Observed	TxR = 0.536	0.641
PA	Width = 0.168	0.432
PI	TxR = 0.458	0.527
Non-breeding range		
Observed	TxR = 0.320	0.418
PA	NPP = 0.393	0.669
PI	Width = 0.123	0.141

The non-phylogenetic components of total and breeding ranges were best correlated with the TxR interaction, again indicating that ranges are smaller than expected based on phylogeny in tropical mountains, with strong positive non-phylogenetic responses in lowlands (Fig. 3b,d). Although the non-phylogenetic component of non-breeding ranges in South America did not have a clear pattern, probably due to the low numbers of species migrating that far south, the pattern in North America suggests a strong non-phylogenetic response to temperature, although across both regions, continental width was the best correlate, albeit very weakly (Table 2). A reanalysis of the region north of 12°N (excluding the outliers in coastal Alaska, Fig. 3f) found that both average temperature and continental width were correlated with the mean non-phylogenetic component ($r = 0.776$ and $r = 0.756$, respectively),but strong covariation between the predictors ($r = 0.857$) makes it difficult to evaluate unambiguously their individual contributions.

Discussion

Range size patterns of oscine passerines closely follow patterns documented for all birds in the New World when viewed in a geographic context, with (relatively) large ranges across Canada and eastern Brazil, moderate ranges across much of the lower USA and tropical South America, and small ranges in Central America, the Andes and the southern tip of South America (Hawkins & Diniz-Filho, 2006; Orme *et al.*, 2006) (see Fig. 2a). Thus, this set of birds seems to follow the same 'rules' that influence all bird ranges. However, examining the different parts of their ranges (total, breeding and non-breeding), as well as partitioning the phylogenetic and non-phylogenetic signals from their ranges adds several novel aspects to understanding range size patterns of this highly mobile group of organisms.

Most previous analyses have focused on breeding ranges only (Hawkins & Diniz-Filho, 2006; Orme *et al.*, 2006) and have found that Rapoport's Rule generally applies within North America, but not across the entire hemisphere, due to birds having large ranges in tropical lowlands. The oscines follow a similar pattern for their breeding ranges (see Fig. 2b). In the Northern Hemisphere broad ranges at high latitudes are believed to reflect a response by species to highly variables temperatures arising from severe cold in the winter (Stevens, 1989), further tempered by recolonisation patterns following the Quaternary ice age cycle (Hewitt, 2000). As also noted by Stevens (1989), migratory birds are not exposed to these winter conditions and so are not expected to follow Rapoport's Rule. However, when considering the total ranges of birds, Rapoport's Rule continues to hold in North America (see Fig. 2a). In hindsight this is not surprising, since all of the migratory species in our dataset leave central and northern Canada in winter (see Fig. 1c), and in doing so substantially increase their range sizes over the entire year relative to non-migratory species. Although the breeding ranges of migratory species may not be particularly large, because unlike residents many have been split into east and west sister species perhaps reflecting migratory divides, low temperatures still strongly influence overall range sizes by driving migratory species southward to escape winter conditions. We found that the non-breeding component of ranges also follows Rapoport's Rule within North America (see Fig. 2c), indicating that it does apply to overwintering populations of migrants. Because few oscine species within South America are long-distance migrants, the differences between total and breeding ranges (see Fig. 2) largely reflect the appearance of the handful of species that migrate into South America from the north, most of which have large non-breeding ranges.

Despite a clear indication that all range size metrics are influenced either directly or indirectly by temperature in the northern hemisphere, across both continents the strongest environmental correlate was the average temperature by spatial range in temperature interaction, a measure of the strength of climatic gradients up the sides of mountains. This almost certainly reflects the strong constraints on the distribution of birds in tropical mountains due to short-distance turnover in local climates and vegetation coupled with topographic complexity generating barriers to dispersal (Ruggiero & Hawkins, 2007; Graham *et al.*, 2010). Given that oscine richness is very high in the tropical Andes and mountains of southern Mexico relative to the lowlands (see Fig. 1a,b), the finding that half of the variation in total and breeding range sizes can be explained by the interaction of macro- and meso-climate (see Table 2) makes sense. Adding additional environmental variables to the regression improves the models somewhat, but the remaining unexplained variation probably reflects the influence of species traits on range sizes. Species distributions, and hence range sizes, are shaped partly by biology (e.g., Buckley, 2010), and dispersal ability has been linked to breeding, non-breeding and total range sizes among 26 warbler species (Böhning-Gaese *et* *al.*, 2006). Obviously, it is the fact that species traits influence ranges sizes, and that these traits may be conserved during cladogenesis, that forms the basis for studies of heritability of range size.

We estimate that phylogenetic relationships among species accounts for up to 15-20% of the species-level variance in breeding and non-breeding ranges, and perhaps one-quarter of the variance in total ranges. A number of analyses of bird clades using a range of methods have found phylogenetic signal of variable strength in range sizes, but the levels identified by PVR fall at the high end of previous results (Waldron, 2007). Whether or not the levels of phylogenetic signal we found are sufficiently large to seriously impact interpretations of range size patterns that do not use a phylogenetically explicit approach is debatable, since the bulk of species-level variation is not phylogenetically structured. We also cannot be certain if the phylogenetic signal is strong enough to require adjustments of type I error when inferential statistics are used to evaluate correlated evolution of range size, although an assumption of independence of the species in our data set would be violated. Our estimates of P may also be inflated slightly, since the null expectations of the PVR are greater than 0, especially for non-breeding ranges. Further, the oscine supertree currently lacks branch lengths, so we have no information on how evolutionary rates may influence range sizes (Price *et al.*, 1997) or our estimates of phylogenetic structure. On the other hand, the PA-components we found do have spatial structure, and their contributions to geographic patterns of range sizes are somewhat stronger than indicated by the species-level analysis.

North and South America show very different spatial patterns of non-phylogenetic vs. phylogenetic signals (see Fig. 3). Although the non-phylogenetic signal is much more strongly correlated with all observed ranges in North America (see Table 1), the phylogenetic component is also positively correlated with observed total and breeding ranges, and partitioning the slopes of ranges on the latitudinal axis increases the contributions of the phylogenetic signals to 18-36%. Thus, in the cold climates associated with North America phylogenetic history has a measurable influence on how species have spread across Canada. Given that all of these species have had to recolonize the region as the ice sheets melted after the last Ice Age, the phylogenetic signal can obviously not reflect the importance of in situ cladogenesis. Instead, closely related species must share traits that have permitted them to track climate change, although the latitudinal position of Old World warblers is thought to be evolutionarily labile (Price *et al.*, 1997). But this does not alter the fact that most of the latitudinally based variation in total and breeding range sizes is non-phylogenetic. This is even more the case for the non-breeding ranges of migratory species (see Fig. 3c). Although there is a tendency for their ranges to be smaller in Central America than in the USA and southern Canada, over 80% of the variation in their winter range sizes is non-phylogenetic.

Bird ranges in South America differ substantially from those in North America in terms of both probable environmental drivers and the extent of phylogenetic signal. For example, all observed range metrics are negatively correlated with average temperature north of 12°N (total r = -0.606, breeding r = -0.559, and non-breeding r = -0.806), but the correlations are positive south of 12°N (total r = 0.578, breeding r = 0.629, and non-breeding r = 0.434). We also found very weak phylogenetic signals in the south for total and breeding range sizes but parity in the strengths of phylogenetic and non-phylogenetic signals for non-breeding ranges (see Table 1). In the latter case it again reflects the effects of the few species in our data set that reach South America but which due to close phylogenetic relationships are expected to share large ranges. For the total and breeding ranges, on the other hand, the fauna comprises species that based on their phylogenetic relationships are expected to have relatively small ranges across the tropics but which in fact have small ranges in the Andes and very large ranges in the lowlands. In the only part of South America subject to seasonally cold winters, the narrowing of the continent prevents positive non-phylogenetic responses to temperature as occurs in North America. Clearly, multiple processes influence range size patterns in North and South America, and this is also true in other parts of the world (Orme *et al.*, 2006).

Although multiple regression models of phylogenetic structure had moderate to high explanatory power (see Table 2), there is little consistency in the primary predictors for the three metrics. This probably reflects that understanding the spatial structure of phylogenetic processes requires knowledge of the traits that influence range size as well as the patterns of environmental gradients. Dispersal ability is likely to be a key trait (Böhning-Gaese *et al.*, 2006), but we currently lack these data across the 423 species in our data set. The models of the non-phylogenetic responses, on the other hand, were slightly more consistent among the range metrics, which because of their strengths are strongly correlated with the observed gradients. Undoubtedly, an approach incorporating species-specific traits will also be needed to understand these patterns as well, although the correlations we find offer some clues. For the moment it is clear that phylogenetic inertia does have a measurable influence on geographic range size patterns, and this is manifested at both the species and biogeographical levels.

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Supporting Information

Additional Supporting Information may be found in:

Appendix S1. List of species with log10 range sizes.
Appendix S2. Correlograms of raw phylogenetic signal in range size across 12 phylogenetic distances classes, with residual signal (S component) after fitting the selected eigenvectors in the PVR.

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Appendix S1

Species list with log$_{10}$- transformed range sizes in parenthesis. Range size metrics indicate total ranges (^{t}), breeding ranges (^{b}) and non-breeding ranges (^{nb}) for migratory species.

Agelaius phoeniceus (7.1487)^{t} (7.1352)^{b} (5.6325)^{nb}, *A. tricolor* (5.0534)^{t} (5.0534)^{b}, *Agelasicus cyanopus* (6.4260)^{t} (6.4260)^{b}, *Agelasticus thilius* (6.4462)^{t} (6.3676)^{b} (5.6655)^{nb}, *Aimophila aestivalis* (6.2404)^{t} (6.2404)^{b}, *A. cassinii* (6.3565)^{t} (6.3080)^{b} (5.3809)^{nb}, *A. ruficeps* (6.0728)^{t} (6.0728)^{b}, *Alopochelidon fucata* (6.6330)^{t} (6.6330)^{b}, *Amblycercus holosericeus* (6.0617)^{t} (6.0617)^{b}, *Amblyramphus holosericeus* (6.1032)^{t} (6.1032)^{b}, *Ammodramus henslowii* (6.2432)^{t} (6.0385)^{b} (5.8182)^{nb}, *A. leconteii* (6.6359)^{t} (6.4575)^{b} (6.1634)^{nb}, *A. savannarum* (6.8969)^{t} (6.7175)^{b} (6.4265)^{nb}, *Amphispiza belli* (6.2658)^{t} (6.0372)^{b} (5.8777)^{nb}, *A. bilineata* (6.3888)^{t} (6.3888)^{b}, *Anthus bogotensis* (5.5263)^{t} (5.5263)^{b}, *A. correndera* (6.4898)^{t} (6.4898)^{b}, *A. furcatus* (6.2983)^{t} (6.2983)^{b}, *A. hellmayri* (6.0609)^{t} (6.0609)^{b}, *A. lutescens* (6.8585)^{t} (6.8585)^{b}, *A. spragueii* (6.4547)^{t} (6.0651)^{b} (6.2273)^{nb}, *Aphelocoma californica* (6.3585)^{t} (6.3585)^{b}, *Atlapetes fulviceps* (4.8900)^{t} (4.8900)^{b}, *A. latinuchus* (5.2494)^{t} (5.2494)^{b}, *A. rufigenis* (4.3288)^{t} (4.3288)^{b}, *A. rufinucha* (4.5912)^{t} (4.5912)^{b}, *A. schistaceus* (5.2066)^{t} (5.2066)^{b}, *Atticora fasciata* (6.8137)^{t} (6.8137)^{b}, *A. melanoleuca* (6.3143)^{t} (6.3143)^{b}, *Baeolophus bicolor* (6.4727)^{t} (6.4727)^{b}, *B. inornatus* (5.2403)^{t} (5.2403)^{b}, *B. wollweberi* (5.7260)^{t} (5.7260)^{b}, *Basileuterus culicivorus* (6.7482)^{t} (6.7482)^{b}, *Buarremon brunneinucha* (5.7902)^{t} (5.7902)^{b}, *Buthraupis montana* (5.4638)^{t} (5.4638)^{b}, *Cacicus cela* (6.9474)^{t} (6.9474)^{b}, *C. chrysonotus* (4.9222)^{t} (4.9222)^{b}, *C. melanicterus* (5.3588)^{t} (5.3588)^{b}, *C. solitarius* (6.9441)^{t} (6.9441)^{b}, *C. uropygialis* (5.6080)^{t} (5.6080)^{b}, *Calamospiza melanocorys* (6.5256)^{t} (6.2622)^{b} (6.1833)^{nb}, *Calcarius mccownii* (6.1779)^{t} (5.8364)^{b} (5.9138)^{nb}, *C. ornatus* (6.3493)^{t} (5.9029)^{b} (6.1571)^{nb}, *C. pictus* (6.2071)^{t} (5.8520)^{b} (5.9542)^{nb}, *Calochaetes coccineus* (4.9963)^{t} (4.9963)^{b}, *Campylorhynchus brunneicapillus* (6.2669)^{t} (6.2669)^{b}, *C. megalopterus* (4.8903)^{t} (4.8903)^{b}, *Cardinalis cardinalis* (6.7660)^{t} (6.7660)^{b}, *C. phoeniceus* (4.8431)^{t} (4.8431)^{b}, *Carduelis atrata* (5.9242)^{t} (5.9242)^{b}, *C. barbata* (6.0464)^{t} (6.0464)^{b}, *C. crassirostris* (5.4620)^{t} (5.4620)^{b}, *C. lawrencei* (5.6440)^{t} (5.1440)^{b} (5.4788)^{nb}, *C. magellanica* (6.7837)^{t} (6.7837)^{b}, *C. notata* (5.6857)^{t} (5.6857)^{b}, *C. olivacea* (5.2384)^{t} (5.2384)^{b}, *C. pinus* (7.1481)^{t} (6.8924)^{b} (6.7963)^{nb}, *C. psaltria* (6.6193)^{t} (6.5942)^{b} (5.3695)^{nb}, *C. spinescens* (5.0684)^{t} (5.0684)^{b}, *C. tristis* (7.0241)^{t} (6.8765)^{b} (6.4837)^{nb}, *C. xanthogastra* (5.1845)^{t} (5.1845)^{b}, *Carpodacus mexicanus* (6.8782)^{t} (6.8782)^{b}, *C. purpureus* (6.8901)^{t} (6.6565)^{b} (6.5091)^{nb}, *Catamblyrhynchus diadema* (5.5202)^{t} (5.5202)^{b}, *Catharus aurantiirostris* (5.8982)^{t} (5.8097)^{b} (5.1643)^{nb}, *C. bicknelli* (5.3719)^{t} (5.1259)^{b} (5.0079)^{nb}, *C. dryas* (5.6683)^{t} (5.6683)^{b}, *C. frantzii* (5.3891)^{t} (5.3891)^{b}, *C. fuscater* (5.4155)^{t} (5.4155)^{b}, *C. fuscescens* (6.6304)^{t} (6.5661)^{b} (5.7695)^{nb}, *C. gracilirostris* (3.5829)^{t} (3.5829)^{b}, *C. guttatus* (7.1017)^{t} (6.9227)^{b} (6.6304)^{nb}, *C. mexicanus* (5.0981)^{t} (5.0981)^{b}, *C. occidentalis* (5.6166)^{t} (5.6166)^{b}, *C. ustulatus* (7.0140)^{t} (6.8777)^{b} (6.4443)^{nb}, *Catherpes mexicanus* (6.6333)^{t} (6.6333)^{b}, *Chlorochrysa phoenicotis* (4.4485)^{t} (4.4485)^{b}, *Chlorophanes spiza* (6.8988)^{t} (6.8988)^{b}, *Chlorornis riefferii* (5.4635)^{t} (5.4635)^{b}, *Chondestes grammacus* (6.8253)^{t} (6.7485)^{b} (6.0351)^{nb}, *Chrysothlypis chrysomelas* (4.1960)^{t} (4.1960)^{b}, *Cichlopsis leucogenys* (5.2857)^{t} (5.2857)^{b}, *Cinclus leucocephalus* (5.7924)^{t} (5.7924)^{b}, *C. mexicanus* (6.6832)^{t} (6.6832)^{b}, *C. schulzi* (4.5666)^{t} (4.5666)^{b}, *Cinnycerthia peruana* (4.8798)^{t} (4.8798)^{b}, *Cissopis leverianus* (6.7182)^{t} (6.7182)^{b}, *Cistothorus palustris* (6.8928)^{t} (6.6862)^{b} (6.4708)^{nb}, *C. platensis* (6.9002)^{t} (6.8117)^{b} (6.1659)^{nb}, *Cnemoscopus rubrirostris* (5.0391)^{t} (5.0390)^{b}, *Coccothraustes vespertinus* (6.9846)^{t} (6.5958)^{b} (6.7565)^{nb}, *Conirostrum albifrons* (5.4743)^{t} (5.4743)^{b}, *C. bicolor* (5.7471)^{t} (5.7471)^{b}, *C. cinereum* (5.6553)^{t} (5.6553)^{b}, *C. ferrugineiventre* (5.1687)^{t} (5.1687)^{b}, *C. speciosum* (6.8583)^{t} (6.8583)^{b}, *Coryphospingus cucullatus* (6.6908)^{t} (6.6067)^{b} (5.9363)^{nb}, *Creurgops dentatus* (5.0412)^{t} (5.0412)^{b}, *C. verticalis* (4.9727)^{t} (4.9727)^{b}, *Curaeus curaeus* (6.0156)^{t} (5.7930)^{b} (5.6188)^{nb}, *Cyanerpes caeruleus* (6.8244)^{t} (6.8244)^{b}, *C. nitidus* (6.4270)^{t} (6.4270)^{b}, *Cyanocitta cristata* (6.8331)^{t} (6.8238)^{b} (5.1598)^{nb}, *C. stelleri* (6.4920)^{t} (6.4920)^{b}, *Cyanocompsa brissonii* (6.7673)^{t} (6.7673)^{b}, *Cyanocorax chrysops* (6.4520)^{t} (6.4520)^{b}, *Cyanolyca viridicyanus* (5.2964)^{t} (5.2964)^{b}, *Cyclarhis gujanensis* (7.1299)^{t} (7.1299)^{b}, *Cypsnagra hirundinacea* (6.5040)^{t} (6.5040)^{b}, *Dacnis cayana* (7.0813)^{t} (7.0813)^{b}, *Delothraupis castaneoventris* (5.1181)^{t} (5.1181)^{b}, *Dendroica coronata* (7.1905)^{t} (6.9939)^{b}

(6.7518)^{nb}, *D. striata* (7.0215)^{t} (6.8018)^{b} (6.6204)^{nb}, *D. tigrina* (6.4973)^{t} (6.4034)^{b} (5.7858)^{nb}, *D. townsendi* (6.3617)^{t} (6.1475)^{b} (5.9521)^{nb}, *Diglossa albilatera* (5.3804)^{t} (5.3804)^{b}, *D. baritula* (5.3683)^{t} (5.3683)^{b}, *D. brunneiventris* (5.5022)^{t} (5.5022)^{b}, *D. carbonaria* (4.8457)^{t} (4.8457)^{b}, *D. duidae* (5.0190)^{t} (5.0190)^{b}, *D. glauca* (5.0599)^{t} (5.0599)^{b}, *D. humeralis* (5.1915)^{t} (5.1915)^{b}, *D. lafresnayii* (5.0402)^{t} (5.0402)^{b}, *D. major* (4.4991)^{t} (4.4991)^{b}, *D. mystacalis* (5.0839)^{t} (5.0839)^{b}, *D. plumbea* (3.9509)^{t} (3.9509)^{b}, *D. sittoides* (5.7735)^{t} (5.7735)^{b}, *D. venezuelensis* (3.4671)^{t} (3.4671)^{b}, *Dives warszewiczi* (5.3346)^{t} (5.3346)^{b}, *Dolichonyx oryzivorus* (6.6793)^{t} (6.5892)^{b} (5.9520)^{nb}, *Dubusia taeniata* (5.4493)^{t} (5.4493)^{b}, *Dumetella carolinensis* (6.9070)^{t} (6.8341)^{b} (6.0962)^{nb}, *Entomodestes coracinus* (4.3226)^{t} (4.3226)^{b}, *E. leucotis* (5.3158)^{t} (5.3158)^{b}, *Eucometis penicillata* (6.7563)^{t} (6.7563)^{b}, *Euphagus carolinus* (7.0008)^{t} (6.8677)^{b} (6.4224)^{nb}, *E. cyanocephalus* (6.9357)^{t} (6.6769)^{b} (6.5879)^{nb}, *Euphonia finschi* (5.5150)^{t} (5.5150)^{b}, *E. laniirostris* (6.6101)^{t} (6.6101)^{b}, *Geothlypis aequinoctialis* (6.8964)^{t} (6.8964)^{b}, *G. trichas* (7.1237)^{t} (7.0460)^{b} (6.3382)^{nb}, *Gnorimopsar chopi* (6.7731)^{t} (6.7731)^{b}, *Gymnomystax mexicanus* (6.1865)^{t} (6.1865)^{b}, *Gymnorhinus cyanocephalus* (6.1262)^{t} (6.1262)^{b}, *Haplochelidon andecola* (5.6871)^{t} (5.6871)^{b}, *Helmitheros vermivorum* (6.4241)^{t} (6.2439)^{b} (5.9549)^{nb}, *Hemispingus atropileus* (5.0803)^{t} (5.0803)^{b}, *H. auricularis* (5.0304)^{t} (5.0304)^{b}, *H. calophrys* (4.3637)^{t} (4.3637)^{b}, *H. frontalis* (5.3028)^{t} (5.3028)^{b}, *H. melanotis* (5.2666)^{t} (5.2666)^{b}, *H. parodii* (4.2967)^{t} (4.2967)^{b}, *H. piurae* (4.0881)^{t} (4.0881)^{b}, *H. rufosuperciliaris* (4.5514)^{t} (4.5514)^{b}, *H. superciliaris* (5.4340)^{t} (5.4340)^{b}, *H. trifasciatus* (4.9149)^{t} (4.9149)^{b}, *H. verticalis* (4.6628)^{t} (4.6628)^{b}, *H. xanthophthalmus* (4.9649)^{t} (4.9649)^{b}, *Hemithraupis flavicollis* (6.7491)^{t} (6.7491)^{b}, *Henicorhina leucosticta* (6.4017)^{t} (6.4017)^{b}, *Heterospingus xanthopygius* (5.1848)^{t} (5.1848)^{b}, *Hylocichla mustelina* (6.6168)^{t} (6.5432)^{b} (5.8097)^{nb}, *Hylophilus ochraceiceps* (6.7810)^{t} (6.7810)^{b}, *H. poicilotis* (5.8466)^{t} (5.8466)^{b}, *Hylorchilus sumichrasti* (4.0613)^{t} (4.0613)^{b}, *Icterus cayanensis* (7.1054)^{t} (7.1054)^{b}, *I. chrysocephalus* (5.8906)^{t} (5.8906)^{b}, *I. cucullatus* (6.1734)^{t} (6.0723)^{b} (5.4907)^{nb}, *I. galbula* (6.8394)^{t} (6.6732)^{b} (6.3418)^{nb}, *I. graceannae* (4.8898)^{t} (4.8898)^{b}, *I. graduacauda* (5.4264)^{t} (5.4264)^{b}, *I. gularis* (5.7479)^{t} (5.7479)^{b}, *I. icterus* (5.6361)^{t} (5.6361)^{b}, *I. jamacaii* (6.3082)^{t} (6.3082)^{b}, *I. maculialatus* (4.9409)^{t} (4.9409)^{b}, *I. mesomelas* (5.9981)^{t} (5.9981)^{b}, *I. nigrogularis* (6.1358)^{t} (6.1358)^{b}, *I. parisorum* (6.2674)^{t} (6.2410)^{b} (5.0392)^{nb}, *I. pectoralis* (5.2910)^{t} (5.2910)^{b}, *I. spurius* (6.7937)^{t} (6.6804)^{b} (6.1547)^{nb}, *I. wagleri* (5.8849)^{t} (5.8392)^{b} (4.8849)^{nb}, *Iridosornis analis* (4.9868)^{t} (4.9868)^{b}, *Ixoreus naevius* (6.5538)^{t} (6.5207)^{b} (5.4189)^{nb}, *Junco hyemalis* (7.2089)^{t} (7.0072)^{b} (6.7788)^{nb}, *J. phaeonotus* (5.6789)^{t} (5.6789)^{b}, *Lampropsar tanagrinus* (6.3830)^{t} (6.3830)^{b}, *Lanio versicolor* (6.4518)^{t} (6.4518)^{b}, *Lanius ludovicianus* (6.9475)^{t} (6.9475)^{b}, *Macroagelaius subalaris* (4.2913)^{t} (4.2913)^{b}, *Melanoptila glabrirostris* (5.1654)^{t} (5.1654)^{b}, *Melanotis caerulescens* (5.6845)^{t} (5.6845)^{b}, *Melospiza georgiana* (6.9730)^{t} (6.7805)^{b} (6.5269)^{nb}, *M. lincolnii* (7.0446)^{t} (6.8784)^{b} (6.5470)^{nb}, *M. melodia* (7.1141)^{t} (7.0134)^{b} (6.4299)^{nb}, *Melozone kieneri* (5.5184)^{t} (5.5184)^{b}, *Microcerculus marginatus* (6.6795)^{t} (6.6795)^{b}, *Mimus patagonicus* (6.2751)^{t} (6.1463)^{b} (5.6844)^{nb}, *M. saturninus* (6.8572)^{t} (6.8572)^{b}, *Molothrus aeneus* (6.3787)^{t} (6.3787)^{b}, *M. ater* (7.0792)^{t} (7.0509)^{b} (5.8783)^{nb}, *M. bonariensis* (7.1275)^{t} (7.1275)^{b}, *M. rufoaxillaris* (6.5030)^{t} (6.5030)^{b}, *Myadestes ralloides* (5.6606)^{t} (5.6606)^{b}, *M. townsendi* (6.7250)^{t} (6.5538)^{b} (6.2379)^{nb}, *M. unicolor* (5.1471)^{t} (5.1471)^{b}, *Nemosia pileata* (6.9396)^{t} (6.9396)^{b}, *Neochelidon tibialis* (6.6208)^{t} (6.6208)^{b}, *Neothraupis fasciata* (6.3501)^{t} (6.3501)^{b}, *Nephelornis oneilli* (4.4843)^{t} (4.4843)^{b}, *Notiochelidon flavipes* (5.1068)^{t} (5.1068)^{b}, *N. murina* (5.6291)^{t} (5.6291)^{b}, *N. pileata* (4.8766)^{t} (4.8766)^{b}, *Ocyalus latirostris* (5.6220)^{t} (5.6220)^{b}, *Odontorchilus cinereus* (6.0203)^{t} (6.0203)^{b}, *Oporornis tolmiei* (6.5507)^{t} (6.4214)^{b} (5.9616)^{nb}, *Oreomanes fraseri* (5.3651)^{t} (5.3651)^{b}, *Oreopsar bolivianus* (4.8887)^{t} (4.8887)^{b}, *Oreoscoptes montanus* (6.5291)^{t} (6.2442)^{b} (6.2113)^{nb}, *Oryzoborus angolensis* (7.0840)^{t} (7.0840)^{b}, *O. crassirostris* (6.4036)^{t} (6.4036)^{b}, *Parula americana* (6.5975)^{t} (6.5255)^{b} (5.7812)^{nb}, *P. gutturalis* (3.5924)^{t} (3.5924)^{b}, *P. pitiayumi* (6.9224)^{t} (6.9224)^{b}, *Passerculus sandwichensis* (7.2552)^{t} (7.1394)^{b} (6.6245)^{nb}, *Passerella iliaca* (7.0311)^{t} (6.8778)^{b} (6.5043)^{nb}, *Passerina amoena* (6.5000)^{t} (6.4509)^{b} (5.5293)^{nb}, *P. ciris* (6.4175)^{t} (6.1491)^{b} (6.0812)^{nb}, *P. cyanea* (6.8618)^{t} (6.7682)^{b} (6.1491)^{nb}, *P. leclancherii* (5.1475)^{t} (5.1475)^{b}, *P. rositae* (3.8693)^{t} (3.8693)^{b}, *P. versicolor* (6.1877)^{t} (6.1381)^{b} (5.2210)^{nb}, *Perisoreus canadensis* (6.8634)^{t} (6.8634)^{b}, *Petrochelidon fulva* (5.9949)^{t} (5.9949)^{b}, *P. pyrrhonota* (7.3748)^{t} (7.0790)^{b} (7.0684)^{nb}, *P. rufocollaris* (5.0408)^{t} (5.0408)^{b}, *Peucedramus taeniatus* (5.8406)^{t} (5.8406)^{b}, *Phainopepla nitens* (6.1532)^{t} (6.0970)^{b} (5.2373)^{nb}, *Pheucticus ludovicianus* (6.7710)^{t} (6.5771)^{b} (6.3274)^{nb}, *Pipilo aberti* (5.2310)^{t} (5.2310)^{b}, *P. albicollis* (4.8106)^{t} (4.8106)^{b}, *P. chlorurus* (6.5957)^{t} (6.2400)^{b} (6.3433)^{nb}, *P. crissalis* (5.5228)^{t} (5.5228)^{b}, *P. erythrophthalmus* (6.5493)^{t} (6.4991)^{b} (5.5877)^{nb}, *P. fuscus* (6.2144)^{t} (6.2144)^{b}, *P. maculatus* (6.6868)^{t} (6.5499)^{b} (6.1187)^{nb}, *P. ocai* (5.0571)^{t} (5.0571)^{b}, *Pipraeidea melanonota* (6.3246)^{t} (6.3246)^{b}, *Platycichla leucops* (5.6167)^{t} (5.6167)^{b}, *Plectro-*

phenax hyperboreus (4.8909)^{t} (3.7304)^{b} (4.8599)^{nb}, *Poecile atricapillus* (6.9454)^{t} (6.9454)^{b}, *P. carolinensis* (6.3641)^{t} (6.3641)^{b}, *P. cincta* (5.4984)^{t} (5.4984)^{b}, *P. gambeli* (6.4307)^{t} (6.4307)^{b}, *P. hudsonica* (6.8514)^{t} (6.8514)^{b}, *P. rufescens* (5.9814)^{t} (5.9814)^{b}, *P. sclateri* (5.3047)^{t} (5.3047)^{b}, *Polioptila albiloris* (5.3436)^{t} (5.3436)^{b}, *P. caerulea* (6.8611)^{t} (6.8184)^{b} (5.8325)^{nb}, *P. californica* (5.1113)^{t} (5.1113)^{b}, *P. melanura* (6.0444)^{t} (6.0444)^{b}, *P. nigriceps* (5.2227)^{t} (5.2227)^{b}, *Pooecetes gramineus* (6.9950)^{t} (6.8042)^{b} (6.5460)^{nb}, *Progne elegans* (6.6162)^{t} (6.1041)^{b} (6.4566)^{nb}, *P. murphyi* (4.7168)^{t} (4.7168)^{b}, *P. sinaloae* (5.2748)^{t} (5.2748)^{b}, *P. subis* (7.2391)^{t} (6.7577)^{b} (7.0651)^{nb}, *P. tapera* (7.1628)^{t} (6.9157)^{b} (6.8003)^{nb}, *Protonotaria citrea* (6.5527)^{t} (6.3371)^{b} (6.1452)^{nb}, *Psarocolius angustifrons* (6.3485)^{t} (6.3485)^{b}, *P. atrovirens* (5.1439)^{t} (5.1439)^{b}, *P. decumanus* (7.0246)^{t} (7.0246)^{b}, *P. wagleri* (5.6828)^{t} (5.6828)^{b}, *Pseudoleistes guirahuro* (6.3380)^{t} (6.3380)^{b}, *P. virescens* (5.9496)^{t} (5.9496)^{b}, *Ptilogonys cinereus* (5.7194)^{t} (5.7194)^{b}, *Pygochelidon cyanoleuca* (7.2477)^{t} (7.0165)^{b} (6.8634)^{nb}, *Pyrrhocoma ruficeps* (5.7865)^{t} (5.7865)^{b}, *Quiscalus lugubris* (5.8455)^{t} (5.8455)^{b}, *Q. mexicanus* (6.6994)^{t} (6.6994)^{b}, *Q. quiscula* (6.9282)^{t} (6.9147)^{b} (5.4133)^{nb}, *Ramphocelus bresilius* (5.5771)^{t} (5.5771)^{b}, *R. carbo* (7.0200)^{t} (7.0200)^{b}, *R. nigrogularis* (6.3226)^{t} (6.3226)^{b}, *R. passerinii* (5.3173)^{t} (5.3173)^{b}, *R. sanguinolentus* (5.3713)^{t} (5.3713)^{b}, *Regulus calendula* (7.1524)^{t} (6.9668)^{b} (6.6938)^{nb}, *R. satrapa* (7.0599)^{t} (6.7975)^{b} (6.7164)^{nb}, *Ridgwayia pinicola* (5.5259)^{t} (5.5259)^{b}, *Salpinctes obsoletus* (6.7437)^{t} (6.7343)^{b} (5.0749)^{nb}, *Saltator atricollis* (6.4388)^{t} (6.4388)^{b}, *S. coerulescens* (7.0057)^{t} (7.0057)^{b}, *Schistochlamys melanopis* (6.7909)^{t} (6.7909)^{b}, *Seiurus aurocapilla* (6.8381)^{t} (6.7179)^{b} (6.2216)^{nb}, *Sericossypha albocristata* (4.8994)^{t} (4.8994)^{b}, *Setophaga ruticilla* (7.0159)^{t} (6.8245)^{b} (6.5679)^{nb}, *Sialia currucoides* (6.7907)^{t} (6.6410)^{b} (6.2555)^{nb}, *S. mexicana* (6.3850)^{t} (6.2504)^{b} (5.8107)^{nb}, *S. sialis* (6.7705)^{t} (6.7371)^{b} (5.6396)^{nb}, *Sicalis luteola* (6.8164)^{t} (6.4333)^{b} (6.5844)^{nb}, *Sitta canadensis* (7.0917)^{t} (6.8540)^{b} (6.7166)^{nb}, *S. carolinensis* (6.9354)^{t} (6.9354)^{b}, *S. pygmaea* (6.2908)^{t} (6.2908)^{b}, *Spiza americana* (6.6984)^{t} (6.5393)^{b} (6.1852)^{nb}, *Spizella arborea* (7.0538)^{t} (6.6973)^{b} (6.8020)^{nb}, *S. atrogularis* (6.1337)^{t} (5.9058)^{b} (5.7448)^{nb}, *S. breweri* (6.6583)^{t} (6.5091)^{b} (6.1220)^{nb}, *S. pallida* (6.6455)^{t} (6.5077)^{b} (6.0799)^{nb}, *S. 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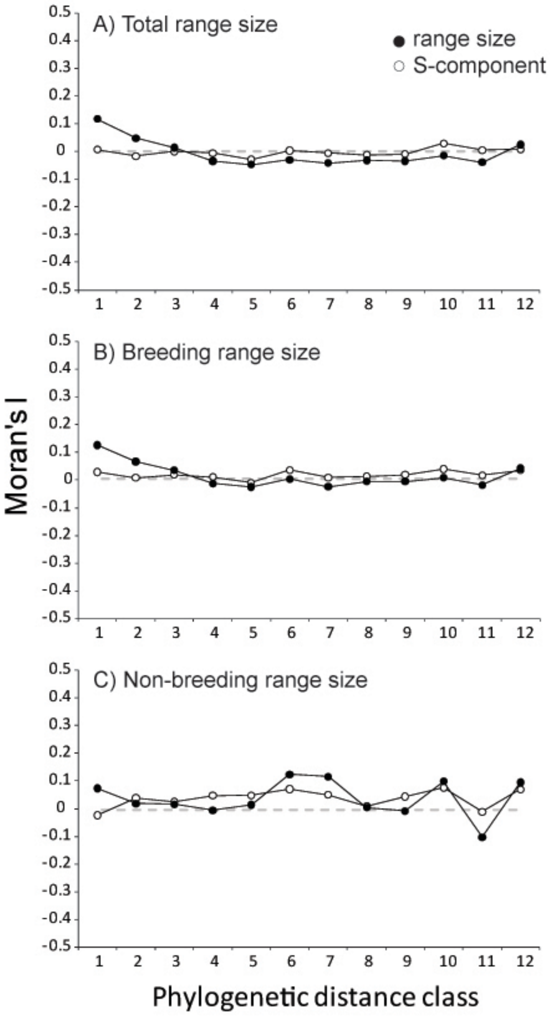
(7.4477)^{t} (7.4003)^{b} (6.4621)^{nb}, *T. ochraceus* (4.2389)^{t} (4.2389)^{b}, *T. rufociliatus* (4.9933)^{t} (4.9933)^{b}, *T. rufulus* (4.7682)^{t} (4.7682)^{b}, *T. solstitialis* (5.7432)^{t} (5.7432)^{b}, *Turdus chiguanco* (6.1553)^{t} (6.1553)^{b}, *T. falcklandii* (5.9940)^{t} (5.9940)^{b}, *T. fuscater* (5.6141)^{t} (5.6141)^{b}, *T. grayi* (6.0253)^{t} (6.0253)^{b}, *T. migratorius* (7.2508)^{t} (7.2162)^{b} (6.1353)^{nb}, *T. rufiventris* (6.7015)^{t} (6.7015)^{b}, *Vermivora celata* (7.0126)^{t} (6.8741)^{b} (6.4491)^{nb}, *V. peregrina* (6.8018)^{t} (6.6792)^{b} (6.1925)^{nb}, *V. ruficapilla* (6.5673)^{t} (6.4429)^{b} (5.9638)^{nb}, *Vireo gilvus* (7.0144)^{t} (6.9917)^{b} (5.7216)^{nb}, *V. huttoni* (6.0844)^{t} (6.0844)^{b}, *V. leucophrys* (5.7597)^{t} (5.7597)^{b}, *V. olivaceus* (7.3652)^{t} (7.0694)^{b} (7.0588)^{nb}, *V. philadelphicus* (6.5345)^{t} (6.4394)^{b} (5.8281)^{nb}, *V. plumbeus* (6.2159)^{t} (6.1119)^{b} (5.5441)^{nb}, *Volatinia jacarina* (7.1832)^{t} (7.1832)^{b}, *Wilsonia canadensis* (6.6893)^{t} (6.4415)^{b} (6.3276)^{nb}, *W. pusilla* (6.9694)^{t} (6.9006)^{b} (6.1353)^{nb}, *Xanthocephalus xanthocephalus* (6.8070)^{t} (6.6773)^{b} (6.2189)^{nb}, *Xanthopsar flavus* (5.7215)^{t} (5.7215)^{b}, *Xenodacnis parina* (5.0404)^{t} (5.0403)^{b}, *Zonotrichia albicollis* (6.9769)^{t} (6.7530)^{b} (6.5821)^{nb}, *Z. atricapilla* (6.3683)^{t} (6.2239)^{b} (5.8197)^{nb}, *Z. leucophrys* (7.1256)^{t} (6.8671)^{b} (6.7773)^{nb}, *Z. querula* (6.4580)^{t} (6.2302)^{b} (6.0687)^{nb}.

Appendix S2

Correlograms of raw phylogenetic signal in range size across 12 phylogenetic distances classes, with residual signal (S component) after fitting the selected eigenvectors in the PVR. (a) Total ranges, (b) breeding ranges and (c) non-breeding ranges. Note that the PVR removed virtually all phylogenetic autocorrelation across all distance class in total and breeding ranges, whereas very low levels (<0.08) remain at some distances in non-breeding ranges.



4. Phylogenetic relationships and Global Bird body size patterns

Ignacio Morales-Castilla, Miguel Á. Rodríguez & Bradford A. Hawkins

Article submitted to *Ecography (In review)*

Capítulo 4

Filogenia basal, productividad primaria y el gradiente global de tamaño corporal de aves

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

MORALES-CASTILLA, I., RODRÍGUEZ, M. Á., and HAWKINS, B. A., Deep phylogeny, net primary productivity and the global bird body size gradient. *In review in Ecography*

Resumen

Aunque el tamaño corporal es un rasgo constreñido evolutivamente, aún no se ha documentado la influencia de las relaciones filogenéticas sobre los gradientes globales de tamaño corporal de aves. En este trabajo cuantificamos y mapeamos la estructura filogenética y no-filogenética del gradiente global del tamaño corporal de aves, explorando el grado en que está condicionado por la inercia filogenética en comparación con mecanismos como la conservación de calor, la disponibilidad de recursos, la conservación de nicho, la resistencia a la escasez de recursos, y la competencia interespecífica. Utilizamos la regresión de autovectores filogenéticos (PVR) para separar el gradiente de tamaño corporal de aves en una componente filogenéticamente autocorrelacionada (PA) y otra filogenéticamente independiente (PI). Empleamos regresiones simples, múltiples y parciales, para investigar las asociaciones existentes entre las componentes PA y PI del tamaño corporal e hipótesis ambientales, y para explorar las contribuciones independiente y combinada de los factores ambientales, la autocorrelación filogenética y la riqueza de especies al gradiente de tamaño corporal. Tres cuartos de la variación 'entre-especies' del tamaño corporal se explican mediante las relaciones filogenéticas a nivel de familia, con hasta un 55% representando inercia filogenética y un 23% posiblemente representando conservación de nicho filogenético. Globalmente, mientras la componente filogenética muestra una asociación más fuerte con la temperatura, la variación filogenéticamente independiente del tamaño está asociada a la productividad primaria, lo que está de acuerdo con la hipótesis de 'resisten-

cia a la escasez de recursos'. Sin embargo encontramos que, en latitudes septentrionales, la conservación de calor tiene una contribución destacada a los patrones no filogenéticos, y también que el Nuevo y el Viejo Mundo muestran patrones geográficos de tamaño muy distintos. Por otro lado, no encontramos asociaciones independientes de la riqueza de especies con el tamaño corporal. En conjunto, concluimos que no existe una explicación única para los gradientes de tamaño corporal a escala global. Específicamente, a pesar de las importantes diferencias regionales aún por resolver, posiblemente relacionadas con los patrones de diversificación de los mayores clados de aves, las relaciones filogenéticas basales y la escasez de recursos en combinación con la conservación del calor y la resistencia a la escasez de recursos, probablemente han interactuado en distintas partes del mundo para dar forma al gradiente global de tamaño corporal de aves que observamos actualmente.

Deep phylogeny, net primary productivity and the global bird body size gradient

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Abstract

Although body size is evolutionarily constrained, the influence of phylogenetic relationships on global body size gradients is undocumented. We quantify and map family-level phylogenetic and non-phylogenetic structure of the global gradient of birds, exploring the extent to which it is influenced by phylogenetic inertia in contrast to mechanisms such as heat conservation, resource availability, niche conservatism, starvation resistance or interspecific competition. We used phylogenetic eigenvector regression (PVR) to partition the global bird body size gradient into its phylogenetically autocorrelated (PA) and phylogenetically independent (PI) components. Simple, piecewise and partial regressions were used to investigate associations between the PA and PI components of body size and environmental hypotheses and explore independent and overlapping contributions of environment, phylogenetic autocorrelation and species richness to the body size gradient. Three-quarters of the cross-species variation in bird body size can be explained by phylogenetic relationships at the family level, with up to 55% representing phylogenetic inertia and 23% perhaps representing phylogenetic niche conservatism. Whereas the phylogenetic component is most strongly associated with temperature, phylogenetically independent variance is most strongly associated with net primary productivity globally, consistent with the 'starvation resistance' hypothesis. However, in northern latitudes heat conservation probably contributes to non-phylogenetic patterns, and the New and Old Worlds have very different patterns. We found no independent association of species richness with body size. We conclude that there is no 'one size fits all' explanation for the body size gradient at the global scale. Despite major unresolved regional differences related to diversification patterns of major bird clades, deep phylogenetic relationships and resource scarceness in combination with heat conservation or with starvation resistance probably operate in concert in shaping the global bird body size gradient in different parts of the world.

Introduction

The pattern of larger body sizes of endotherms toward the poles proposed by Bergmann (1847) is amongst the most studied by macroecologists (Blackburn *et al.* 1999, Rodríguez *et al.* 2006, 2008). A variety of approaches have been used (i.e. intraspecific, cross-species and assemblage-based), and their differences and advantages have been evaluated (see Blackburn and Hawkins 2004, Gaston *et al.* 2008, Olalla-Tárraga *et al.* 2010, Adams and Church 2011). Although the method used can influence the interpretation of results (Ruggiero and Hawkins 2006), it is common for explanations derived from one approach being used to explain the outcomes of a different approach (see Gaston *et al.* 2008). For instance, even when a physiological mechanism may explain intraspecific variation in body size across space, it does not necessary account for geographical trends in body sizes of multi-species assemblages.

The study of body size from an assemblage perspective is most appropriate to identify the geographical structure of patterns and processes (Ruggiero and Hawkins 2006, Olalla-Tárraga *et al.* 2010) and has been used to document body size gradients of both ectotherms and endotherms, including insects (Cushman *et al.* 1993, Hawkins 1995, Hawkins and Lawton 1995, Chown and Klok 2003, Kaspari 2005), fish (Knouft 2002), amphibians (Olalla-Tárraga and Rodríguez 2007, Olalla-Tárraga *et al.* 2009, 2010), reptiles (Olalla-Tárraga *et al.* 2006), birds (Blackburn and Gaston 1996, Ramirez *et al.* 2008, Olson *et al.* 2009), and mammals (Blackburn and Hawkins 2004, Rodríguez *et al.* 2006, 2008, Diniz-Filho *et al.* 2009). But although taxonomically extensive databases of geographical patterns of body size are being generated, underlying mechanisms remain subject to debate. This is not surprising in a field where manipulative experiments at the appropriate taxonomic and geographic scale are not possible.

Recent assemblage-based studies of birds have validated the generality of Bergmann's rule in the Northern Hemisphere for the New World (Ramirez *et al.* 2008) and globally (Olson *et al.* 2009). In both studies, temperature was found to be the single strongest correlate of body size, whereas variables related to resource availability (e.g. vegetation, measured by either actual evapotranspiration or the normalized difference vegetation index) were less strongly associated with gradients. Comparing the correlations of these environmental variables with body size gradients is of interest because they can be linked to proposed explanations for Bergmann-like patterns for endotherms: the heat conservation hypothesis –large-bodied species are favoured in cold climates because their reduced surface-area-to-volume-ratios (Bergmann 1847, Hamilton 1961, James 1970), and/or thicker insulation layers (Blackburn *et al.* 1999) give them a higher tolerance to cold; the resource availability hypothesis –body size increases along with productivity because resource availability sets a limit to the body size an animal can reach (Rosenzweig 1968, Geist 1987); and the starvation resistance (or fasting endurance) hypothesis – larger animals are favoured in seasonal and unpredictable environments because they metabolize fat stores at lower weight-specific rates and, thus, withstand starvation better than smaller animals (Lindsey 1966, Calder 1984, Lindstedt and Boyce 1985, Cushman *et al.* 1993). It is important to note that these hypotheses are not mutually exclusive (e.g. Olson *et al.* 2009), and that they were originally generated from the results of intra-specific and cross-species studies and, hence, need not apply equally to assemblage-based body size gradients.

Additional potential influences on body size gradients from an assemblage perspective include species richness, acting via more intense interspecific competition in species-rich environments (Blackburn and Gaston 1996, Cardillo 2002, Olson *et al.* 2009), and species turnover in space, acting via differential diversification of clades with different body sizes (Olson *et al.* 2009) or differential colonization of deglaciated areas after the Pleistocene (Blackburn and Hawkins 2004, Rodríguez *et al.* 2006). Diversification patterns themselves represent a set of processes reflected in phylogenetic relationships among species that can arise multiple ways, including early colonization of an environment followed by in situ radiation (see Blackburn *et al.* 1999), or local extirpation of clades comprising similarly sized species. This has been explored to some extent for birds by examining changes in body size patterns across multiple taxonomic levels (Olson *et al.* 2009). However, although Olson *et al.* (2009) have shown that macroevolutionary processes and species turnover have influenced the global bird body size gradient, it remains unknown if phylogenetic patterns of body size have responded to the same environmental drivers as patterns arising from responses of birds independent of their evolutionary history.

Here we use phylogenetic eigenvector regression (PVR) to quantify and map the phylogenetic and non-phylogenetic structure of the global bird body size gradient, based on the pattern of phylogenetic autocorrelation among bird families. We also evaluate in so far as possible using a correlative approach three widely studied hypotheses for body size patterns, heat conservation as measured by temperature, resource availability as measured by net primary productivity (NPP) and resistance to starvation, evaluated using seasonal variation in actual evapotranspiration as a proxy of within year variability in resource availability (Ramirez *et al.* 2008). Further, we revisit the proposal by Olson *et al.* (2009) that species richness directly influences bird body size gradients. Finally, our approach allows us to compare relationships between environmental gradients and phylogenetic autocorrelation, including patterns unrelated to measured environmental gradients (interpreted by some as phylogenetic inertia, Desdevises *et al.* 2003), environmental signal independent of phylogeny, and environmentally structured phylogenetic signal (phylogenetic niche conservatism sensu Desdevises *et al.* 2003). Our spatial approach is hierarchical; we first analyze the global pattern, followed by a New World vs. Old World contrast to document interregional differences.

Material and Methods

The data

Maps of bird breeding ranges on continental landmasses (sources provided in Hawkins *et al.* 2007) were projected onto a global Behrmann equal-area grid comprising 9,319 km2 cells, which after removal of small coastal cells and cells supporting fewer than 20 bird species resulted in 12,639 cells for analysis. Islands were also excluded (except for Great Britain and Tierra del Fuego), because different constraints on body size may operate on islands (e.g., the Island Rule, Lomolino *et al.* 2006). Afghanistan was excluded because we could locate no range maps for the country.

Body masses were obtained from a large number of sources and log10-transformed for 7,518 species of terrestrial birds (the species checklist and body masses are provided in Appendix S1). For 461 species (6%), direct mass data were not available, and we used linear regressions of mass against length for species in the same genus or family to estimate body mass (see Ramirez *et al.* 2008). For 28 species (<0.4%) neither mass nor length data were available, so we assigned family mean masses. Body masses of sexually dimorphic species were averaged over both genders. To confirm that inclusion of indirect body sizes for some species did not affect our results, we correlated the spatial pattern of the phylogenetically independent components (see below) with and without these species and found virtually identical patterns globally (r = 0.980).

The temperature variable used to evaluate the heat conservation hypothesis was derived from BIO1 [Mean Annual Temperature, (TEMP)] in the WORLDCLIM database (Hijmans *et al.* 2005). Resource availability was evaluated with average gridded values of annual net primary productivity (NPP), extracted from Imhoff *et al.* (2004) (data available at: http://sedac.ciesin.columbia.edu/es/hanpp.html, accessed January, 2011). Additionally, the Ahn and Tateishi (1994) global dataset was used to generate gridded values of actual evapotranspiration (AET), annual values of which were strongly correlated with NPP (r = 0.910). Starvation resistance was evaluated using seasonal range in actual evapotranspiration (rAET), computed as the absolute difference between January and July AET. Species richness within cells was calculated from the range maps.

Phylogenetic analysis

A species-level supertree for all birds does not yet exist, so we used a family-level phylogeny combining the non-passerine part of Sibley and Ahlquist (1990) phylogeny and the Barker *et al.* (2004) phylogeny for passerines (for evaluations of the robustness of this phylogenetic combination see Hawkins *et al.* 2005, 2006). A total of 122 bird families were analysed, and log10-transformed body masses of the species in each family were averaged for the phylogenetic analysis. Three families comprising four species were excluded because their extreme body masses distorted patterns and destabilized statistical models: Struthionidae, Rheidae and Casuaridae.

Phylogenetic eigenvector regression (PVR, Diniz-Filho *et al.* 1998) was used to partition the phylogenetically autocorrelated (PA) and phylogenetically independent (PI) components of bird body size. This method transforms a pairwise phylogenetic distance matrix, in our case based on the numbers of nodes separating families (e.g. Montoya *et al.* 2008, Ramirez *et al.* 2008), into phylogenetic eigenvectors through a

Principal Coordinate Analysis (PCoA). In principle, the use of node counting to define phylogenetic distances, implicitly assumes a 'speciational' model for the evolution of the trait. However we found that at least for a family level phylogeny, defining phylogenetic distances based on numbers of nodes instead of branch lengths does not alter our results (see Fig. S1). The goal of PVR is to regress a biotic trait (i.e. bird body size in our case) against representative eigenvectors (sensu Diniz-Filho *et al.* 2011) to generate values predicted by the pattern of phylogenetic autocorrelation among taxa and residuals representing sources of variation after removing the autocorrelation (Diniz-Filho *et al.* 1998, 2007, 2009, Martins *et al.* 2002, Ramirez *et al.* 2008). Hence, PVR controls for taxon-level phylogenetic autocorrelation in a trait due to its pattern rather than the underlying process. Although a number of process-based approaches to understanding correlated evolution have been developed, PVR has the advantages of flexibility when the underlying evolutionary process is unknown or complex, and it allows the predicted values of the trait to be converted to assemblage level averages and mapped (Diniz-Filho *et al.* 2011), something that process-based methods cannot accomplish as they are currently developed.

PVR has been criticised because of the lack of a hypothesized process, and because all eigenvectors would be necessary to take the entire phylogeny into account, which would result in a perfect fit (R2=1) and thus leave no residual variation in which to investigate associations with other variables (Rohlf 2001). But, unless the trait under study had evolved according to a Brownian Motion (BM) model (J. A. F. Diniz Filho, T. F. Rangel, T. Santos, and L. M. Bini unpublished manuscript), not all eigenvectors are necessary to model trait variation among taxa, only those that account for the existing phylogenetic autocorrelation in the trait (Diniz-Filho *et al.* 2011). Thus, to determine if bird family body size evolution is Brownian, we used Blomberg's K, a phylogenetic signal metric with an expected value of 1.0 under BM (Blomberg *et al.* 2003, see also Revell *et al.* 2008 for additional details). We found a phylogenetic signal significantly higher than 1 (Blomberg's K = 1.824, p<0.005), which supports the use of PVR in this case. Accordingly, we followed Diniz-Filho *et al.* (2011) and selected representative phylogenetic eigenvectors using the optimization algorithm developed by Griffith and Peres-Neto (2006) in the spatial context. This procedure generates successive regression models of the trait against the phylogenetic eigenvectors, and selects at each step the eigenvector that reduces the largest amount of residual phylogenetic autocorrelation. As new eigenvectors are added to the regression, residuals are updated and autocorrelation recalculated. The search stops when residual autocorrelation is reduced below an arbitrary autocorrelation threshold (Moran's I <0.05 in our case). As an additional test, we built a phylogenetic correlogram to check how effective this procedure was in removing phylogenetic autocorrelation in bird family body size across phylogenetic distances.

Since PVR's metric of phylogenetic signal is its R2, and the R2 of regression models increases along with the number of explanatory variables included in them (even if these variables were composed by random numbers), part of the phylogenetic signal measured by PVR will inevitably reflect the number of selected eigenvectors. To quantify how much this effect affected our estimation of phylogenetic signal, we randomly reshuffled mean family body masses across the phylogeny 1,000 times, regressed each of these random samples against the set of selected phylogenetic eigenvectors, and then computed the mean and standard error of the resulting R2 distribution, which we compared against the observed R2.

Following Diniz-Filho *et al.* (2011) we also used phylogenetic generalized least-squares to generate a PGLS transform of mean family log10-body size (Z-vector) comprising the body size values that would be expected if species were phylogenetically independent (see Diniz-Filho *et al.* 2011 for technical details). This Z-vector is the PGLS equivalent to the PVR's PI-component and allowed us to evaluate the extent to which the patterns were consistent across methods.

Finally, we assigned the PA- and PI- component values given by PVR for each family to its constituent species and then calculated their mean values in the grid cells to compare their spatial patterns and examine associations with environmental gradients and species richness (e.g. Diniz-Filho *et al.* 2009). It should be noted that because we used a family-level phylogeny to examine species-level body sizes, the PI-component will contain any phylogenetic signal occurring below the family level. The magnitude of lower-level phylogenetic autocorrrelation is expected to be small, given that about 90% of the variation in bird life history traits is explained at the family level (Bennett and Owens 2002). Even so, we explored the potential extent of low-level phylogenetic signal in body size among endotherms using body sizes of New World mammals coupled with a widely used species-level supertree (Bininda-Emonds *et al.* 2007). As for the case of birds (see below), more than two thirds of the phylogenetic signal in mammal body size occurred at the family level, while only an extra 6% was captured when taxonomic resolution was increased to the species level (Table S2). Although we cannot directly test this for birds, available evidence for both birds and mammals suggests that for endotherms using less than fully resolved trees to measure phylogenetic autocorrelation in body masses does not greatly underestimate its magnitude.

Statistical analysis

Just as the hypotheses we investigate are not mutually exclusive explanations for body size patterns, the predictors we use to evaluate them are not orthogonal, but collinear to varying degrees (rTEMP vs. NPP = 0.493, rTEMP vs. rAET = 0.087, and rNPP vs. rAET = 0.219). Variation partitioning based on partial regression has been designed to be applied in these situations (see Legendre and Legendre 1998), for which we used two- and three-way partial ordinary least squares (OLS) to explore relationships between the observed mean log10 body sizes in the cells and the three environmental variables (TEMP, NPP and rAET) at global extent, and in the New and Old Worlds. The same techniques were also used to investigate associations for the mean-PA and mean-PI values. In all cases, our goal was to isolate the unique and shared components in variation of mean body size associated with the predictors to evaluate the extent to which each variable (and the hypothesis to which it was linked), either individually or in concert with other variables, could underlay the observed patterns. Although a correlative approach can never unambiguously resolve the problem of which hypotheses constitute true explanations for mean body size patterns, it s quantifies indirectly to what extent this could be the case.

On the other hand, given both the broad geographical extents of our analyses and the use of a grid-based approach, the occurrence of spatial autocorrelation in the data is guaranteed at varying scales. Although it is well known that spatial autocorrelation does not bias OLS regression coefficients (Cressie 1993, Fortin and Dale 2005, Schabenberg and Gotway 2005), and that autocorrelation is not an issue for OLS regression unless when using inferential statistics (i.e. p-values), which we avoid here, we also acknowledged that spatial autocorrelation is a matter of concern to some workers. Consequently, we evaluated the robustness of the coefficients of determination (i.e. of the elements used for variation partitioning analysis) of our global, and

New and Old Words models by comparing them with those obtained from subsampled sets in which positive spatial autocorrelation was forced to be low. For this we ran a randomization procedure in which we randomly selected cells for each region imposing the constraint that the cells had to be separated by at least 1,000 km. There were two reasons for this. First, because the amount of positive autocorrelation in the residuals of our environmental models begun to decrease sharply beyond this distance (Moran's I values became ≤0.2 in all cases). And second, because unlike larger distances, this allowed generating subsamples with reasonably large sample sizes (100 cells for the global extent, and 50 cells for the New and Old Worlds). Thus, we generated 100 random subsamples per region, repeated the partial regression analysis for each of them, computed the mean coefficient of determination value per subsample set, and then used t-tests to compare these means with the coefficients of determination obtained for the complete datasets.

We also employed piecewise regression if visual inspection of scatter plots of mean size (or of mean-PA or mean-PI) against environmental predictors revealed an inflection point in the relationships. However, we took into account that scarce data at the extremes of the scatter plots may cause the appearance of spurious inflection points (i.e. without biological meaning), so we only retained a piecewise regression if its coefficient of determination was at least 5% higher than that of its linear counterpart.

Finally, based on Desdevises *et al.* (2003) we used three-way partial regression to partition the global and New and Old Wold bird body size gradients into the proportion of the variation accounted for by (1) phylogenetic autocorrelation independent of both the environmental gradients captured by our three environmental variables and species richness (assumed to estimate phylogenetic inertia); (2) the component comprising variation due to environment independent of phylogeny and species richness (within-lineage adaptation); (3) the spatially structured phylogenetic components (an estimate of phylogenetic niche conservatism); and (4) the direct contribution of species richness to the gradient independent of phylogenetic relationships and environment. Also, the non-phylogenetic component was partitioned using a two-way partial regression to quantify covariation of environment and bird species richness.

Results

Phylogenetic signal in bird body sizes

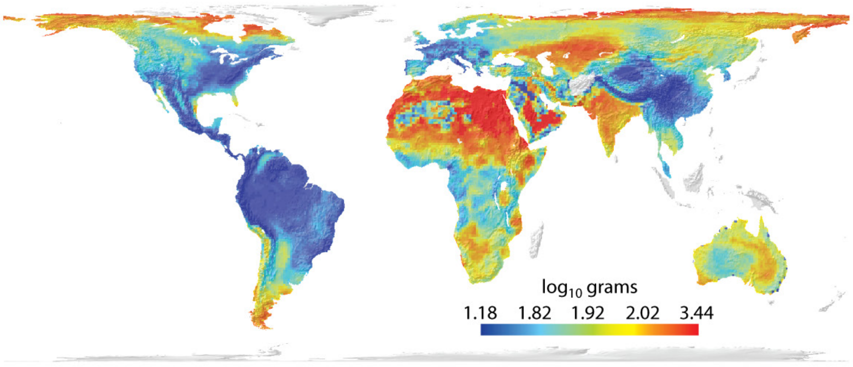
Body sizes among families show positive phylogenetic autocorrelation at short phylogenetic distances (i.e. for closely related families) becoming negative or null at opposite ends of the tree (Fig. S2). The 17 selected phylogenetic eigenvectors predicted much of the variation in body size at the family level ($R^2 = 0.688$) and this was significantly greater than a random expectation (R^2null = 0.131, $p<0.001$). Residuals from the PVR (the PI-component) contained minimal phylogenetic autocorrelation at all phylogenetic distances, indicating that variation in this component is independent of phylogeny at the family level (see Fig. S2). Also, comparison of the PI-component with the Z-vector obtained through PGLS indicated that they reflect similar trends, either when comparing their values across families, and geographically after averaging their respective values in the cells (see Fig. S3). This indicates that the patterns we found are robust independently of the method. Overall, these results indicate that approximately two-thirds of the variation in body masses among bird families is linked to a combination of phylogenetic inertia and phylogenetic niche conservatism.

Phylogenetic and non-phylogenetic contributions to the global body size gradient

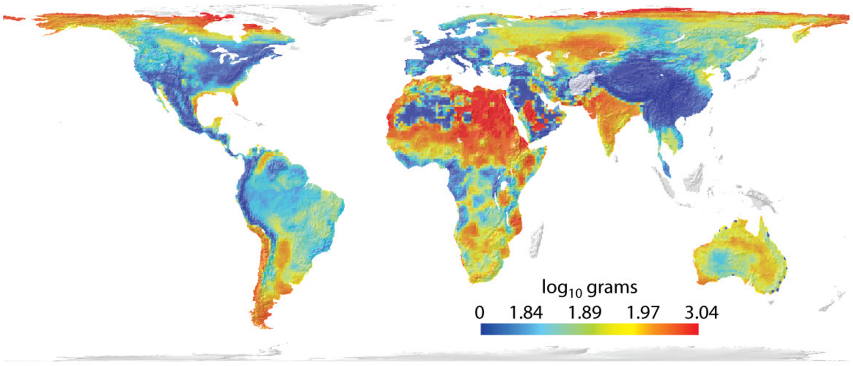
The global body size pattern is very similar to that reported by Olson *et al.* (2009), although we do not share identical data sources, and we use means of log10 body masses rather than medians (Fig. 1a). As expected given the strong phylogenetic signal in body size at the family level, a very similar pattern was found for mean-PA values (Fig. 1b), which in turn were strongly correlated with mean observed body sizes ($r = 0.867$). On the other hand, mean-PI values showed a clear latitudinal gradient in the New World with greater positive deviations from body sizes predicted by phylogeny toward the north and south (Fig. 1c).

Average divergence from a phylogenetic expectation was negative (i.e. body sizes smaller than expected) for most of the Neotropics and southern Nearctic. In the Old World, patterns were geographically complex, with species larger than expected in the

(a) Observed mean log body size



(b) Mean PA-component



(c) Mean PI-component

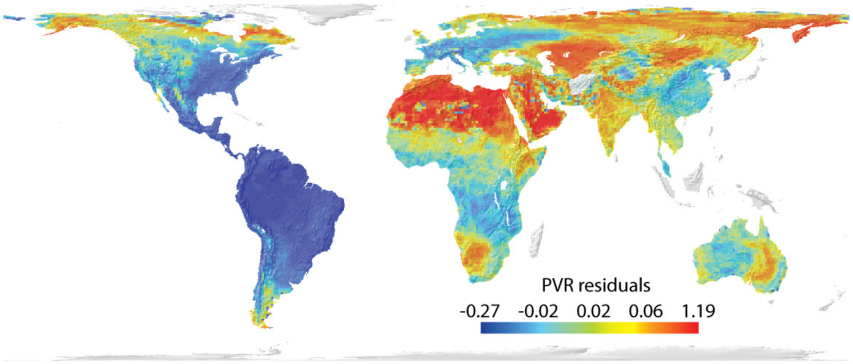


Figure 1. Geographical patterns of (a) mean body size, and of mean values of the (b) phylogenetically autocorrelated [PA] and non-phylogenetic [PI] components of body size obtained through a PVR analysis of 7,518 bird species. Units are log10 body masses in grams. Note that the values for the PI-component can be negative since they are the residuals from a PVR regression and averaged over all species in a cell.

Saharan, Arabic, Kalahari, Namibian, Kara-Kun, Takla Makan and Gobi De serts, as well as in the Himalayas, India and the Australian central lowlands. Negative to null expectations were found in central Europe, tropical Africa, the Yangtze River basin and the Australian western plateau. Mean-PI values were also correlated with mean body sizes globally (r = 0.755), but not as strongly as were mean-PA values, and the correlation between mean-PA and mean-PI was weakly positively correlated (r = 0.328), suggesting largely independent responses to current environmental gradients.

Major regional differences in the relationships of the components to the observed gradient were also apparent. In the Old World the observed gradient was strongly correlated with mean-PA (r = 0.933) and less so with mean-PI (r = 0.661), that is, the observed body size pattern is largely due to spatial variation in the phylogenetic composition of the avifaunas. In the New World the observed gradient was a more even mix of phylogenetic and non-phylogenetic components (r = 0.831 for mean-PA and r = 0.817 for mean-PI).

Environmental predictors of body size patterns and their PI- and PA components

In the New World, average values of body size and its phylogenetically independent (PI) component were strongly negatively associated with both temperature (Fig. 2a,i) and net primary productivity (Fig. 2c,k). In contrast, in the Old World, simple regressions of mean body size and mean-PI against temperature and productivity were weaker (Fig. 2b-j, d-l). There, body size and its PA-component appear to decrease with increasing temperature only in cold and temperate areas (below ~-8ºC), with a reversal at higher temperatures, reflecting larger sizes in the deserts (Fig. 2b,f).

The relationship between the phylogenetically autocorrelated portion of body size and temperature had two distinctive domains in the New World (Fig. 2e), with mean-PA values increasing towards colder areas in the first domain, but being independent of temperature (New World) in warmer areas. This non-linearity was confirmed by piecewise regression, which showed substantially better fit (Fig. 2e) than its linear counterpart (r^2New = 0.158).

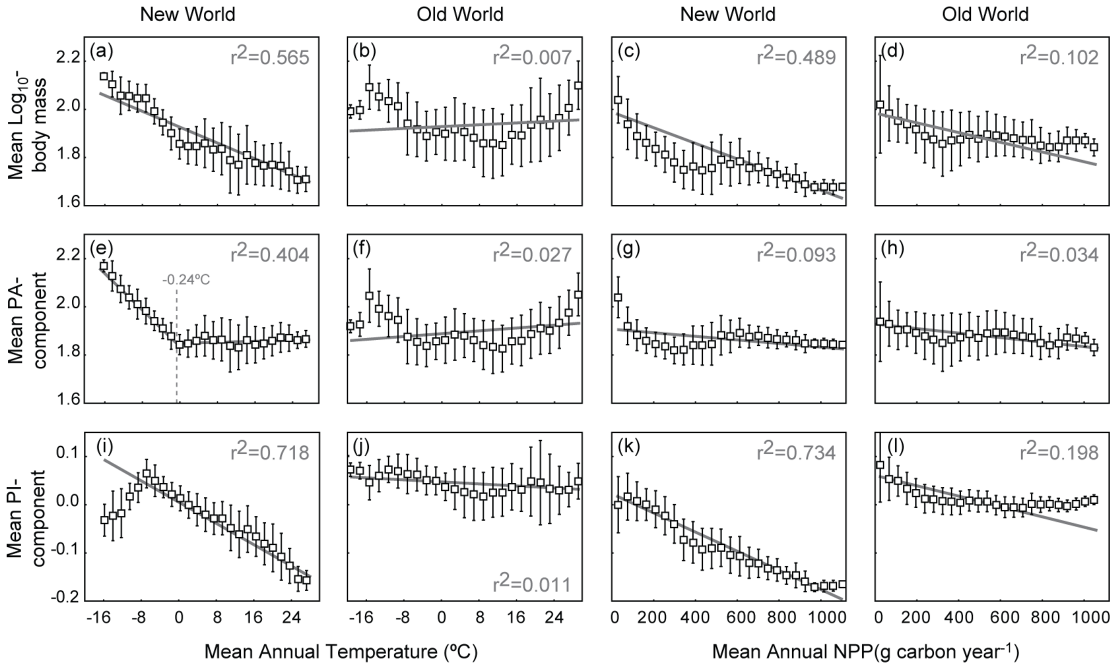
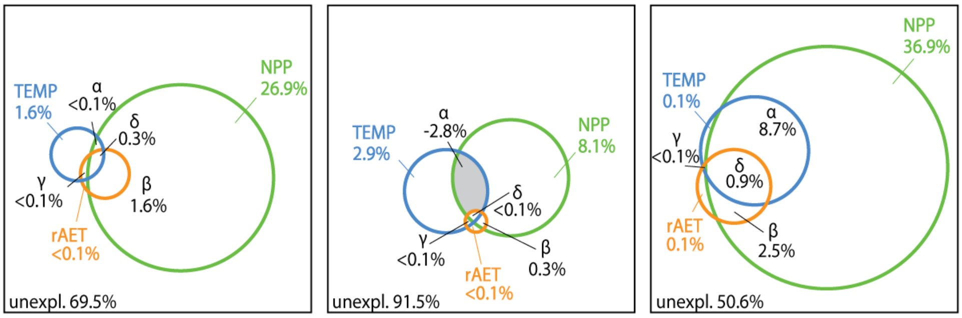


Figure 2. Relationships of (a-d) mean observed log10-body size, (e-h) mean-PA (the phylogenetically autocorrelated component of body size) and (i-l) mean-PI (non-phylogenetic component) with annual temperature and NPP for the New World and the Old World. For representation purposes the data were divided into 25 equal-range categories of the variable in the abscissa and the average (±SD) value of each category provided. Coefficients of determination (r2) and regression lines of OLS regressions are shown. Piecewise regression fitted to the relationship between the mean-PA and temperature (e) identified a temperature breakpoint for the New World (-0.24 ºC).

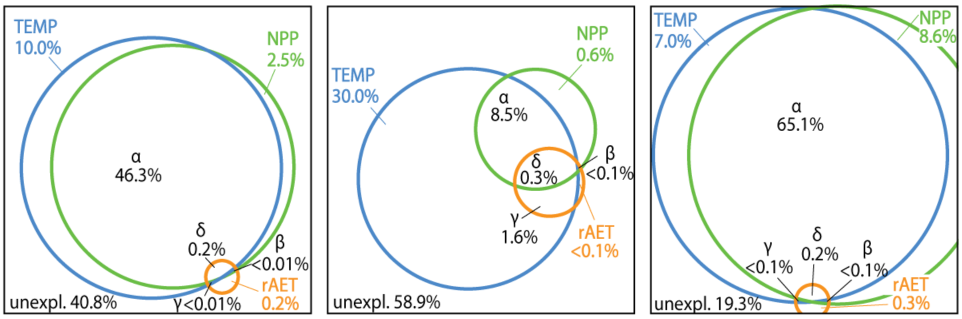
Globally, three-way partial regressions revealed productivity as the predictor more strongly associated with body size and the PA- and PI-components (Fig. 3a-c). A similar pattern held for the Old World (Fig. 3g,i), whereas for the New World temperature accounted for more variation in body size and mean-PA, but productivity still explained more geographical variation of mean-PI than temperature (Fig. 3d-f). Accounting for nonlinear relationships of mean-PA with temperature increased the explanatory power of the model in the New World (from $R^2 = 0.065$ to $R^2 = 0.300$, Fig. 3e). It is notable that even though the relative contribution of seasonality (i.e. rAET) was marginal in all cases (Fig. 3a-h) its independent and overlapping relationships



(a) Global Body Size

(b) Global PA-component

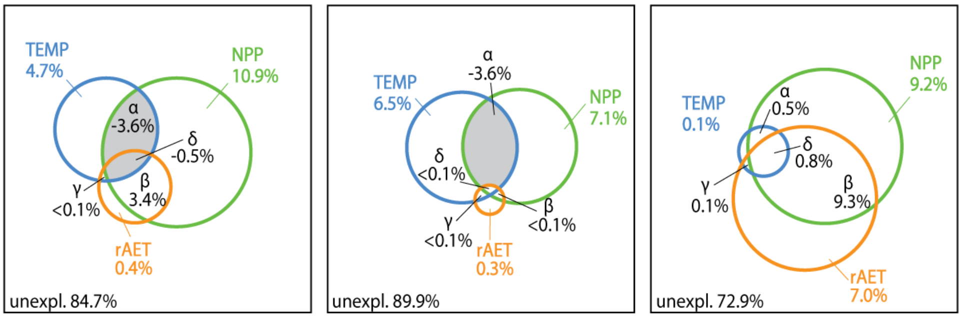
(c) Global PI-component



(d) New World Body Size

(e) New World PA-component

(f) New World PI-component



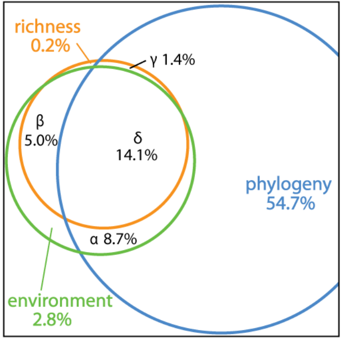
(g) Old World Body Size

(h) Old World PA-component

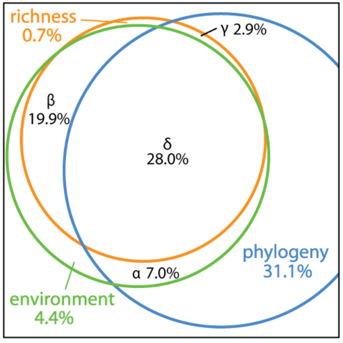
(i) Old World PI-component

Figure 3. Venn diagrams for environmental three-way partial regressions showing the independent and overlapping relationships of mean annual temperature (TEMP), net primary productivity (NPP) and seasonal range in actual evapotranspiration (rAET) and variation in mean log10-body size, mean-PA and mean-PI globally (a, b, c), the New World (d, e, f) and the Old World (g, h, i). Lower case Greek letters indicate overlapping proportions of variation of TEMP and NPP (α), NPP and rAET (β), TEMP and rAET (γ) and among the three variables (δ). Regions shaded in gray indicate negative values due to interactions among variables.

(a) Global



(b) New World



(c) Old World

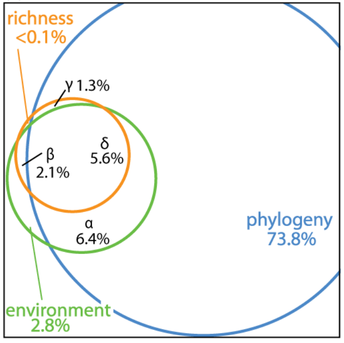


Figure 4. Venn diagrams for three-way partial regressions showing the independent and overlapping contributions of environment (i.e. TEMP, NPP and rAET combined), phylogeny and species richness on explaining the variance in mean log10-body size (a) globally (b) in the New World and (c) in the Old World. The proportion of variation explained independently by phylogeny is interpreted as phylogenetic inertia, whereas the overlapping variation between phylogeny and environment encompasses niche conservatism (sensu Desdevises *et al.* 2003). Lower case Greek letters indicate overlapping of variation of phylogeny and environment (α), environment and richness (β), phylogeny and richness (γ) and among the three variables (δ).

with productivity were larger for the Old World's PI-component, possibly reflecting selection of larger sizes driven by deserts. Overall, environmental models were stronger for mean-PI than for mean-PA either at the global context ($R^2 = 0.494$ vs. $R^2 = 0.085$), in the New World ($R^2 = 0.807$ vs. $R^2 = 0.175$) or in the Old World ($R^2 = 0.270$ vs. $R^2 = 0.101$). In all cases productivity and its collinear association with temperature are the main correlates of mean-PI, i.e., of the portion of the body size gradient independent of familial phylogenetic relationships. As expected, none of these results were affected by spatial autocorrelation in the full data (Fig. S4).

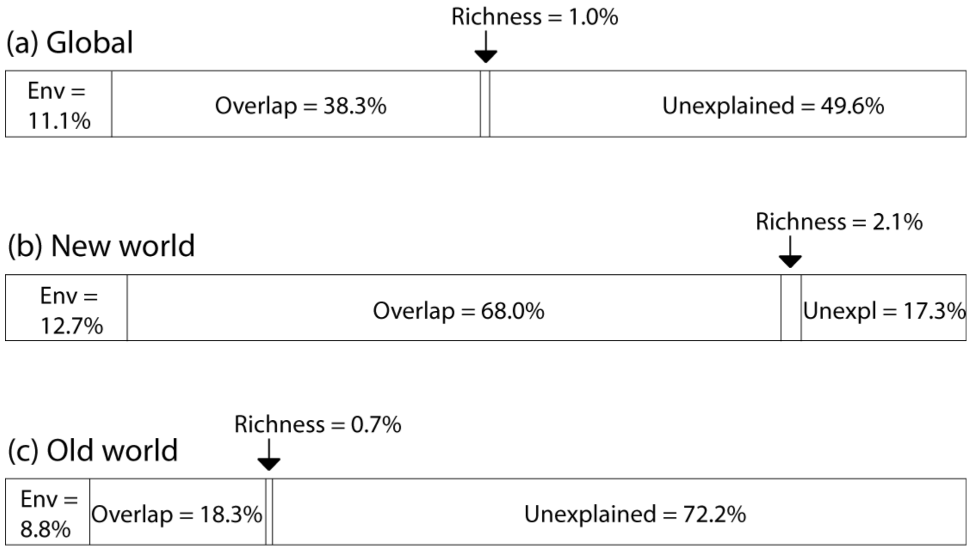


Figure 5. Partial regression showing relative contributions of environment (TEMP, NPP and rAET combined) and species richness to the variation in mean values of the non-phylogenetic [PI]component of body size (a) globally, (b) in the New World and (c) in the Old World.

Species richness, phylogenetic inertia and phylogenetic niche conservatism

Although species richness has been hypothesized to represent a primary driver of global body size gradients (Olson *et al.* 2009), and correlations of richness with mean both body size ($r = 0.493$) and mean-PI ($r = 0.627$) were moderately strong in our data as well, partial regressions indicated that most of the variation associated with species richness is collinear with that associated with climate whether for the body size gradient (Fig. 4) or mean-PI (Fig. 5). Therefore, the independent relationships of species richness and body size were virtually nil in both the phylogenetic and non-phylogenetic components (all $R^2<0.021$, Fig. 4 and 5), and we cannot conclude unambiguously that biotic interactions associated with the number of potential competitor species have influenced spatial body size gradients of birds.

Most of the variation in the spatial body size gradient was independently accounted for by phylogeny, suggesting strong phylogenetic inertia at all extents (Fig. 4). Variable levels of co-variation between phylogeny and environment suggest substantial niche conservatism of body size in the New World, but much less in the Old World.

Discussion

Higher-level phylogenetic relationships explain a substantial proportion of the global bird body size gradient, up to two thirds of the total variation in the gradient can be predicted by the phylogenetic structure of avian families. This is consistent with previous analyses for birds (Ramirez *et al.* 2008), carnivores (Gittleman *et al.* 1996, Diniz-Filho and Tôrres 2002, Diniz-Filho *et al.* 2009, Freckleton and Jetz 2009), Plethodon salamanders (Olalla-Tárraga *et al.* 2010), and with general strong phylogenetic constraints on body size (Freckleton *et al.* 2002, Blomberg *et al.* 2003). Clearly, future work focused on body size patterns such as Bergmann's Rule will need to consider phylogenetic structure in the data as either a pattern or a process.

Patterns of mean-PA, phylogenetic inertia and niche conservatism

To the extent that phylogenetic inertia operating independently of environmental drivers and niche conservatism generating covariance between the trait and environmental gradients (Desdevises *et al.* 2003, Diniz-Filho and Bini 2008) can be partitioned by partial regression methods, our results potentially identify phylogenetic inertia at the family level as the dominant component at the global extent. On the other hand, there is clear spatial variation in the relationships between the phylogenetic component of body size and environment: in regions with cold climates, mean-PA shows moderately strong relationships with temperature in the New World (see Fig. 2e). Given that most of Canada was under a kilometre of ice during the most recent Ice Age, the current body size gradient in the northern half of North America is consistent with a pattern of recolonization following glacial retreat, suggesting a link between body size and dispersal ability that is also phylogenetically conserved at the family level. There are a number of potential reasons why the relationship might partially occur in the Old World (see Fig. 2f), which was not as extensively glaciated, but we lack the data to evaluate them. Irrespective, the patterns suggest a leading role for temperature on the phylogenetic structure of body size in areas with very cold climates.

The non-phylogenetic component and hypotheses for body size

Approximately a third in the variance of the bird body size gradient is independent of the phylogenetic relationships among families. However, evaluating processes such as the heat conservation hypothesis proposed by Bergmann (1847) requires removing the influence of phylogenetic relatedness in order to assess responses of species to environmental clines, which unfortunately we can do only partially in the absence of a species level supertree.

Globally, the non-phylogenetic responses of species body size to environment appear to be fundamentally driven by decreasing primary productivity (see Fig. 3c). Thus, our results are inconsistent with the resource availability hypothesis (Rosenzweig 1968), since mean body size is negatively correlated with primary productivity. Despite collinearity between the relationships of temperature and productivity with body size, temperature is not strong predictor of body size across all climates, a pattern also known for mammals (Rodríguez *et al.* 2006, 2008). On the other hand, major differences between the New and Old Worlds indicate that non-phylogenetic patterns are not easy to interpret.

The strong collinearity between productivity and temperature makes interpretation of the patterns in the PI-component in the New World difficult (see Fig. 3f). This is unavoidable because in the New World the least productive areas are primarily the coldest. On contrast, non-phylogenetic patterns in the Old World are associated with productivity, either its annual value (NPP) or the degree of seasonality (rAET), and there is almost no association with temperature (see Fig. 3i). This reflects that the Old World contains extensive non-polar deserts (with low productivity and high temperatures), and also a more seasonal climate outside those deserts. The pattern of larger body sizes in areas of low productivity is clear not only in the most extensive deserts but also in smaller ones, including the Namibian and Kalahari Deserts in Africa, and the Kara-Kun and Takla Makan Deserts in Asia (see Fig. 1c). Thus, although all associations between body size and environment are weak, the resistance to starvation hypothesis (Calder 1984, Lindstedt and Boyce 1985, Cushman *et al.* 1993) is most consistent with the patterns in the Old World (Geist 1987, Zeveloff and Boyce 1988). At the very least, the heat conservation hypothesis can be dismissed across the Old World (see Fig. 2b,j).

Our results partially contradict Olson *et al.* (2009), who identified temperature as the strongest predictor of body size and concluded that productivity plays a secondary role. We found that once family-level phylogenetic autocorrelation is removed, productivity explains substantially more of the variance in the body size gradient. Our results cannot be directly compared to those of Olson *et al.* (2009), since the goodness of fit of their models or the independent relationships of their predictors with body size were not reported. Our modelling approach also had a different goal; our intent was primarily not to predict body size values given environmental conditions, but to assess the degree to which phylogenetic structure constrains the bird body size gradient and to evaluate the extent to which environment is associated with phylogenetic and non-phylogenetic components of global body size patterns.

Conclusions

A major aspect of our analysis is that it is unlikely that a single, global explanation for bird body size gradients exists, whether in a phylogenetic or non-phylogenetic context. While the New World shows a clear Bergmann-like gradient in both North and South America, body size patterns in the Old World are complex (see Fig. 1a) and largely independent of major environmental gradients (see Fig. 2). Although identifying the sources of this geographic complexity will not be easy, we agree with Olson *et* *al.* (2009) that it will almost certainly require a detailed understanding of the deep evolutionary history of the major bird clades and geographic patterns of diversification. The phylogenetic signal in body sizes is very strong, even given that we may have underestimated its strength by excluding any autocorrelation below the family level. After removing the family-level autocorrelation we find that decreasing productivity in conjunction with decreasing temperature (in the New World) or increasing seasonality (in the Old World) are most closely associated with body size gradients. While hypotheses for body size gradients are often viewed as mutually exclusive alternatives, it is likely that resistance to starvation and heat conservation are both operating, albeit in different parts of the world. On the other hand, we find no evidence that biotic interactions associated with species richness patterns have any independent effect on bird body size patterns, but given that richness is itself strongly influenced by climate, disentangling their contributions is challenging. Despite over 160 years of research on body size gradients, we still do not have a clear picture of the drivers of global body size patterns, but at least we are developing a clearer picture of what we are trying to explain.

Acknoledgements

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Supporting Information

Additional Supporting Information may be found in:

Table S1. Bird species checklist and their body masses
Table S2. Comparison of phylogenetic signals in body size between family, genus and species levels for the New World mammals.
Figure S1. Comparison between branch lengths and node counting as methods measuring the phylogenetic distances among bird families.

Figure S2. Phylogenetic correlograms showing Moran's I coefficients for the body size of 122 bird families.
Figure S3. Comparison of results from PVR with PGLS
Figure S4. Tests of potential influence of spatial autocorrelation on coefficients of determination of environmental OLS regression models.

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Appendix S1

Table S1. Species list with body sizes in grams indicated in parenthesis.

Accipiter badius (132.0); *A. bicolor* (301.0); *A. brevipes* (188.0); *A. castanilius* (160.0); *A. chilensis* (368.0); *A. chionogaster* (76.0); *A. cirrhocephalus* (172.0); *A. collaris* (154.4); *A. cooperii* (439.0); *A. erythronemius* (125.0); *A. erythropus* (115.0); *A. fasciatus* (381.0); *A. gentilis* (902.0); *A. gularis* (222.0); *A. melanoleucus* (699.0); *A. minullus* (88.4); *A. nisus* (238.0); *A. novaehollandiae* (376.0); *A. ovampensis* (195.0); *A. poliogaster* (215.0); *A. rufiventris* (198.0); *A. soloensis* (166.0); *A. striatus* (136.0); *A. superciliosus* (104.0); *A. tachiro* (292.0); *A. trivirgatus* (276.0); *A. ventralis* (233.0); *A. virgatus* (116.0); *Aegypius monachus* (9625.0); *A. occipitalis* (4700.0); *A. tracheliotus* (6600.0); *Aquila audax* (3466.0); *A. chrysaetos* (4264.0); *A. clanga* (2206.0); *A. heliaca* (3215.0); *A. nipalensis* (2746.0); *A. pomarina* (1370.0); *A. rapax* (2250.0); *A. verreauxi* (4195.0); *A. wahlbergi* (640.0); *Aviceda cuculoides* (277.0); *A. jerdoni* (363.0); *A. leuphotes* (196.0); *A. subcristata* (327.0); *Busarellus nigricollis* (650.0); *Butastur indicus* (415.0); *B. liventer* (338.0); *B. rufipennis* (335.0); *B. teesa* (325.0); *Buteo albicaudatus* (886.0); *B. albigula* (482.1); *B. albonotatus* (757.0); *B. auguralis* (670.0); *B. brachyurus* (511.0); *B. buteo* (727.0); *B. hemilasius* (1375.0); *B. jamaicensis* (1111.0); *B. lagopus* (956.0); *B. leucorrhous* (290.0); *B. lineatus* (607.0); *B. magnirostris* (269.0); *B. nitidus* (529.0); *B. oreophilus* (700.0); *B. platypterus* (455.0); *B. polyosoma* (788.0); *B. regalis* (1470.0); *B. rufinus* (1175.0); *B. rufofuscus* (1530.0); *B. swainsoni* (959.0); *B. ventralis* (1194.0); *Buteogallus aequinoctialis* (660.0); *B. anthracinus* (996.0); *B. meridionalis* (808.0); *B. urubitinga* (1157.0); *Chondrohierax uncinatus* (287.0); *Circaetus cinerascens* (2048.0); *C. cinereus* (2048.0); *C. fasciolatus* (1017.0); *C. gallicus* (1700.0); *Circus aeruginosus* (712.0); *C. approximans* (755.0); *C. assimilis* (568.0); *C. buffoni* (517.0); *C. cinereus* (406.0); *C. cyaneus* (401.0); *C. macrourus* (389.0); *C. maurus* (509.0); *C. melanoleucos* (340.0); *C. pygargus* (316.0); *C. ranivorus* (507.0); *C. spilonotus* (562.0); *Dryotriorchis spectabilis* (1045.0); *Elanoides forficatus* (417.0); *Elanus axillaris* (271.0); *E. caeruleus* (261.0); *E. leucurus* (346.0); *E. scriptus* (316.0); *Erythrotriorchis radiatus* (870.0); *Gampsonyx swainsonii* (92.9); *Geranoaetus melanoleucus* (2463.0); *Geranospiza caerulescens* (304.0); *Gypaetus barbatus* (5466.0); *Gypohierax angolensis* (1600.0); *Gyps africanus* (5515.0); *G. bengalensis* (4385.0); *G. coprotheres* (8177.0); *G. fulvus* (7436.0); *G. himalayensis* (10000.0); *G. indicus* (5515.0); *G. rueppellii* (7400.0); *Haliaeetus albicilla* (4793.0); *H. leucocephalus* (4740.0); *H. leucogaster* (2865.0); *H. leucoryphus* (2902.0); *H. pelagicus* (7757.0); *H. vocifer* (2807.0); *Haliastur indus* (529.0); *H. sphenurus* (753.0); *Hamirostra melanosternon* (1196.0); *Harpagus bidentatus* (219.0); *H. diodon* (200.0); *Harpia harpyja* (6550.0); *Harpyhaliaetus coronatus* (2950.0); *H. solitarius* (3000.0); *Hieraaetus dubius* (827.0); *H. fasciatus* (2000.0); *H. kienerii* (799.0); *H. morphnoides* (791.0); *H. pennatus* (835.0); *H. spilogaster* (1475.0); *Ichthyophaga humilis* (782.0); *I. ichthyaetus* (2038.0); *Ictinaetus malayensis* (1300.0); *Ictinia mississippiensis* (278.0); *I. plumbea* (250.0); *Kaupifalco monogrammicus* (281.0); *Leptodon cayanensis* (474.0); *L. forbesi* (577.0); *Leucopternis albicollis* (710.0); *L. kuhli* (354.0); *L. lacernulata* (572.4); *L. melanops* (327.0); *L. occidentalis* (660.0); *L. plumbea* (482.0); *L. polionota* (696.9); *L. princeps* (1000.0); *L. schistacea* (1000.0); *L. semiplumbea* (288.0); *Lophaetus occipitalis* (1067.0); *Lophoictinia isura* (586.0); *Machaerhamphus alcinus* (650.0); *Melierax canorus* (675.0); *M. metabates* (705.0); *Micronisus gabar* (178.0); *Milvus lineatus* (836.0); *M. migrans* (567.0); *M. milvus* (1080.0); *Morphnus guianensis* (1750.0); *Necrosyrtes monachus* (2043.0); *Neophron percnopterus* (1892.0); *Oroaetus isidori* (1948.3); *Parabuteo unicinctus* (865.0); *Pernis apivorus* (758.0); *P. ptilorhynchus* (1126.0); *Polemaetus bellicosus* (4063.0); *Polyboroides typus* (638.0); *Rostrhamus hamatus* (426.0); *R. sociabilis* (371.0); *Sarcogyps calvus* (4550.0); *Spilornis cheela* (931.0); *Spizaetus africanus* (1047.0); *S. alboniger* (830.0); *S. cirrhatus* (1480.0); *S. nanus* (560.0); *S. nipalensis* (3013.0); *S. ornatus* (1215.0); *S. tyrannus* (1013.0); *Spizastur melanoleucus* (850.0); *Stephanoaetus coronatus* (3640.0); *Terathopius ecaudatus* (2200.0); *Torgos tracheliotus* (6969.0); *Urotriorchis macrourus* (492.0); *Chelictinia riocourii* (110.0); *Aegithalos bonvaloti* (6.9); *A. caudatus* (8.6); *A. concinnus* (6.1); *A. fuliginosus* (6.0); *A. iouschistos* (7.0); *A. leucogenys* (6.8); *A. niveogularis* (7.8); *Psaltriparus minimus* (5.3); *Aegotheles cristatus* (42.8); *Alaemon alaudipes* (43.9); *A. hamertoni* (44.0); *Alauda arvensis* (37.5); *A. gulgula* (26.3); *Ammomanes cincturus* (18.8); *A. deserti* (25.1); *A. grayi* (22.5); *A. phoenicurus* (26.2); *Calandrella acutirostris* (20.3); *C. brachydactyla* (19.0); *C. cheleensis* (22.2); *C. cinerea* (23.7);

C. raytal (18.5); *C. rufescens* (24.1); *C. somalica* (22.0); *Calendrella pispoletta* (22.5); *Certhilauda albescens* (30.6); *C. burra* (37.5); *C. chuana* (44.1); *C. curvirostris* (24.0); *C. erythrochlamys* (28.1); *Chersomanes albofasciata* (24.7); *Chersophilus duponti* (39.4); *Eremalauda dunni* (20.5); *E. starki* (18.5); *Eremophila alpestris* (33.0); *E. bilopha* (38.5); *Eremopterix australis* (14.2); *E. grisea* (16.0); *E. leucopareia* (14.6); *E. leucotis* (14.5); *E. nigriceps* (14.0); *E. signata* (15.7); *E. verticalis* (17.0); *Galerida cristata* (41.8); *G. deva* (20.0); *G. magnirostris* (41.6); *G. malabarica* (36.8); *G. modesta* (20.2); *G. theklae* (38.2); *Heteromirafra archeri* (26.0); *H. ruddi* (26.6); *Lullula arborea* (26.9); *Melanocorphya bimaculata* (54.1); *M. leucoptera* (45.3); *M. yeltoniensis* (60.1); *Melanocorypha calandra* (61.6); *M. maxima* (75.0); *M. mongolica* (54.2); *Mirafra africana* (45.3); *M. africanoides* (23.3); *M. albicauda* (22.2); *M. angolensis* (36.3); *M. apiata* (27.0); *M. assamica* (26.2); *M. cantillans* (18.7); *M. cheniana* (24.0); *M. collaris* (22.0); *M. cordofanica* (24.0); *M. erythroptera* (21.3); *M. gilletti* (22.4); *M. hypermetra* (61.4); *M. javanica* (23.0); *M. passerina* (24.7); *M. poecilosterna* (24.4); *M. pulpa* (21.9); *M. rufa* (24.0); *M. rufocinnamomea* (26.3); *M. sabota* (24.2); *M. somalica* (46.6); *M. williamsi* (22.0); *Pinarocorys erythropygia* (30.1); *P. nigricans* (38.2); *Pseudalaemon fremantlii* (23.5); *Ramphocoris clotbey* (49.3); *Spizocorys conirostris* (14.3); *S. fringillaris* (19.2); *S. obbiensis* (13.6); *S. personata* (19.7); *Spizpcorys sclateri* (19.0); *Alcedo atthis* (31.4); *A. azurea* (34.9); *A. cristata* (15.7); *A. euryzona* (43.3); *A. hercules* (47.0); *A. leucogaster* (14.5); *A. meninting* (20.6); *A. pusilla* (13.2); *A. quadribrachys* (34.9); *A. semitorquata* (48.0); *Ceyx erithacus* (18.0); *C. lecontei* (9.5); *C. rufidorsa* (17.6); *Ispidina picta* (12.8); *Aix galericulata* (570.0); *A. sponsa* (658.0); *Alopochen aegyptiacus* (1787.0); *Amazonetta brasiliensis* (500.0); *Anas acuta* (947.0); *A. americana* (756.0); *A. andium* (405.0); *A. bahamensis* (519.0); *A. capensis* (402.0); *A. castanea* (625.0); *A. clypeata* (613.0); *A. crecca* (324.0); *A. cyanoptera* (378.0); *A. discors* (360.0); *A. erythrorhyncha* (560.0); *A. falcata* (649.0); *A. flavirostris* (434.0); *A. formosa* (434.0); *A. fulvigula* (989.0); *A. georgica* (584.0); *A. gracilis* (491.0); *A. hottentota* (280.0); *A. penelope* (772.0); *A. platalea* (466.0); *A. platyrhynchos* (2562.0); *A. poecilorhyncha* (1011.0); *A. puna* (554.0); *A. querquedula* (326.0); *A. rhynchotis* (667.0); *A. rubripes* (1250.0); *A. sibilatrix* (934.0); *A. smithii* (592.0); *A. sparsa* (983.0); *A. strepera* (917.0); *A. superciliosa* (1074.0); *A. undulata* (1008.0); *A. versicolor* (617.0); *Anser albifrons* (3637.0); *A. anser* (3309.0); *A. cygnoides* (3513.0); *A. erythropus* (1761.0); *A. fabalis* (2771.0); *A. indicus* (2225.0); *A. rossii* (1500.0); *Aythya affinis* (820.0); *A. americana* (1077.0); *A. australis* (870.0); *A. baeri* (683.0); *A. collaris* (705.0); *A. ferina* (823.0); *A. fuligula* (702.0); *A. marila* (1007.0); *A. nyroca* (574.0); *A. valisineria* (1203.0); *Biziura lobata* (1975.0); *Branta bernicla* (1300.0); *B. canadensis* (3703.0); *B. leucopsis* (1687.0); *B. rufficollis* (1235.0); *Bucephala albeola* (404.0); *B. clangula* (939.0); *B. islandica* (941.0); *Cairina moschata* (2450.0); *C. scutulata* (3000.0); *Callonetta leucophrys* (366.0); *Chen caerulescens* (2631.0); *C. canagica* (2148.0); *Chenonetta jubata* (808.0); *Chloephaga melanoptera* (2037.0); *C. picta* (2889.0); *C. poliocephala* (2025.0); *C. rubidiceps* (2086.0); *Clangula hyemalis* (873.0); *Coscoroba coscoroba* (4327.0); *Cyanochen cyanopterus* (1520.0); *Cygnus atratus* (5650.0); *C. buccinator* (11100.0); *C. columbianus* (6400.0); *C. cygnus* (9350.0); *C. melanocorypha* (4775.0); *C. olor* (10735.0); *Heteronetta atricapilla* (539.0); *Histrionicus histrionicus* (564.0); *Lophodytes cucullatus* (617.0); *Lophonetta specularioides* (787.0); *Malacorhynchus membranaceus* (374.0); *Marmaronetta angustirostris* (477.0); *Melanitta fusca* (1790.0); *M. nigra* (1052.0); *M. perspicillata* (1098.0); *Merganetta armata* (406.0); *Mergellus albellus* (610.0); *Mergus merganser* (1471.0); *M. octosetaceus* (983.0); *M. serrator* (1022.0); *M. squamatus* (1234.0); *Neochen jubata* (1250.0); *Netta erythrophthalma* (800.0); *N. peposaca* (1000.0); *N. rufina* (1118.0); *Nettapus auritus* (266.0); *N. coromandelianus* (392.0); *N. pulchellus* (307.0); *Nomonyx dominicus* (366.0); *Oxyura australis* (798.0); *O. ferruginea* (784.0); *O. jamaicensis* (609.0); *O. leucocephala* (665.0); *O. maccoa* (687.0); *O. vittata* (643.0); *Plectropterus gambensis* (3869.0); *Pteronetta hartlaubii* (290.0); *Sarkidiornis melanotos* (2368.0); *Somateria fischeri* (1559.0); *S. spectabilis* (1618.0); *S. stelleri* (808.0); *Speculanas specularis* (1618.0); *Stictonetta naevosa* (906.0); *Tachyeres leucocephalus* (3013.0); *T. patachonicus* (2831.0); *T. pteneres* (4772.0); *Tadorna cana* (1182.0); *T. cristata* (1500.0); *T. ferruginea* (1242.0); *T. radjah* (887.0); *T. tadorna* (1152.0); *T. tadornoides* (1425.0); *Anhima cornuta* (3150.0); *Chauna chavaria* (2604.0); *C. torquata* (4400.0); *Anhinga anhinga* (1235.0); *A. melanogaster* (1495.0); *A. rufa* (1397.0); *Anseranas semipalmata* (2419.0); *Aeronautes andecolus* (17.8); *A. montivagus* (20.2); *A. saxatalis* (32.1); *Apus acuticauda* (38.7); *A. affinis* (22.6); *A. apus* (37.6); *A. barbatus* (42.8); *A. batesi* (23.0); *A. berliozi* (38.2); *A. bradfieldi* (42.4); *A. caffer* (22.1); *A. horus* (27.5); *A. melba* (26.4); *A. niansae* (32.5); *A. nipalensis* (30.4); *A. pacificus* (45.3); *A. pallidus* (39.9); *Chaetura brachyura* (18.3); *C. chapmani* (23.9); *C. cinereiventris* (13.9); *C. egregia* (23.4); *C. fumosa* (19.4); *C. meridionalis* (22.2); *C. ocypetes* (20.0); *C. pelagica* (23.6); *C. spinicauda* (15.7); *C. vauxi* (17.1); *C. viridipennis* (23.0); *Collocalia* *brevirostris* (12.5); *C. esculenta* (6.4); *C. fuciphaga* (8.8); *C. germani* (13.5); *C. maxima* (12.8); *C. spodiopygius* (6.8); *C. unicolor* (11.0); *Cypseloides cherriei* (22.1); *C. cryptus* (35.3); *C. fumigatus* (42.0); *C. lemosi* (28.1); *C. niger* (39.9); *C. phelpsi* (21.8); *C. rothschildi* (42.0); *C. rutilus* (20.2); *C. senex* (83.8); *C. storeri* (39.5); *Cypsiurus balasiensis* (9.2); *C. parvus* (13.6); *Hirundapus caudacutus* (95.5); *H. cochinchinensis* (83.8); *H. giganteus* (127.0); *Neafrapus boehmi* (14.5); *N. cassini* (40.0); *Panyptila cayennensis* (21.1); *P. sanctihieronymi* (48.1); *Rhaphidura sabini* (16.0); *Schoutedenapus myioptilus* (23.5); *S. schoutedeni* (22.0); *Streptoprocne biscutata* (96.5); *S. semicollaris* (175.0); *S. zonaris* (87.5); *Tachornis furcata* (6.5); *T. squamata* (11.0); *Tachymarptis aequatorialis* (92.8); *Telacanthura melanopygia* (52.0); *T. ussheri* (32.7); *Zoonavena sylvatica* (18.0); *Agamia agami* (567.0); *Ardea cinerea* (1443.0); *A. cocoi* (2253.0); *A. goliath* (4468.0); *A. herodias* (2544.0); *A. insignis* (4000.0); *A. intermedia* (600.0); *A. melanocephala* (1060.0); *A. pacifica* (881.0); *A. picata* (249.0); *A. purpurea* (970.0); *A. sumatrana* (2024.0); *Ardeola bacchus* (306.0); *A. grayii* (253.0); *A. idea* (287.0); *A. ralloides* (287.0); *A. rufiventris* (229.0); *A. speciosa* (181.0); *Botaurus lentiginosus* (706.0); *B. pinnatus* (839.0); *B. poiciloptilus* (1111.0); *B. stellaris* (1325.0); *Bubulcus ibis* (366.0); *Butorides striatus* (184.0); *B. virescens* (212.0); *Casmerodius albus* (874.0); *Cochlearius cochlearius* (645.0); *Dupetor flavicollis* (318.0); *Egretta ardesiaca* (324.0); *E. caerulea* (340.0); *E. eulophotes* (470.0); *E. garzetta* (312.0); *E. gularis* (400.0); *E. novaehollandiae* (560.0); *E. rufescens* (614.0); *E. thula* (371.0); *E. tricolor* (375.0); *E. vinaceigula* (288.0); *Gorsachius leuconotus* (400.0); *G. magnificus* (467.0); *G. melanolophus* (414.0); *Ixobrychus cinnamomeus* (127.0); *I. eurhythmus* (142.0); *I. exilis* (86.3); *I. involucris* (80.1); *I. minutus* (101.0); *I. sinensis* (94.3); *I. sturmii* (133.0); *Mesophoyx intermedia* (500.0); *Nyctanassa violacea* (683.0); *Nycticorax caledonicus* (856.0); *N. nycticorax* (810.0); *Pilherodius pileatus* (570.0); *Syrigma sibilatrix* (463.0); *Tigriornis leucolophus* (750.0); *Tigrisoma fasciatum* (850.0); *T. lineatum* (813.0); *T. mexicanum* (1160.0); *Zebrilus undulatus* (123.0); *Batrachostomus auritus* (206.0); *B. affinis* (50.0); *B. hodgsoni* (51.0); *B. moniliger* (52.8); *B. stellatus* (52.1); *Bombycilla cedrorum* (31.6); *B. garrulus* (54.5); *B. japonica* (42.3); *Phainopepla nitens* (22.1); *Phainoptila melanoxantha* (56.0); *Ptilogonys caudatus* (36.3); *P. cinereus* (33.6); *Bucco capensis* (54.0); *B. macrodactylus* (25.0); *B. noanamae* (38.8); *B. tamatia* (35.5); *Chelidoptera tenebrosa* (35.9); *Hapaloptila castanea* (80.6); *Hypnelus ruficollis* (49.9); *Malacoptila fulvogularis* (57.4); *M. fusca* (45.4); *M. mystacalis* (49.0); *M. panamensis* (42.6); *M. rufa* (48.3); *M. semicincta* (44.0); *M. striata* (44.1); *Micromonacha lanceolata* (19.8); *Monasa atra* (90.4); *M. flavirostris* (62.8); *M. morphoeus* (89.5); *M. nigrifrons* (80.7); *Nonnula amaurocephala* (15.5); *N. brunnea* (22.1); *N. frontalis* (15.7); *N. rubecula* (18.4); *N. ruficapilla* (22.0); *N. sclateri* (16.0); *Notharchus macrorhynchos* (95.9); *N. ordii* (52.8); *N. pectoralis* (69.1); *N. tectus* (26.8); *Nystalus chacuru* (52.3); *N. maculatus* (42.0); *N. radiatus* (61.0); *N. striatipectus* (55.3); *N. striolatus* (47.0); *Aceros comatus* (1470.0); *A. corrugatus* (1590.0); *A. nipalensis* (2385.0); *A. subruficollis* (2042.0); *A. undulatus* (2233.0); *Anorrhinus galeritus* (1172.0); *A. tickelli* (796.0); *Anthracoceros albirostris* (787.0); *A. coronatus* (809.0); *A. malayanus* (1050.0); *Buceros bicornis* (2799.0); *B. rhinoceros* (2380.0); *B. vigil* (2893.0); *Ceratogymna atrata* (1204.0); *C. brevis* (1235.0); *C. bucinator* (644.0); *C. cylindricus* (921.0); *C. elata* (1925.0); *C. fistulator* (510.0); *C. subcylindricus* (1201.0); *Ocyceros birostris* (375.0); *O. griseus* (292.0); *Tockus albocristatus* (290.0); *T. alboterminatus* (225.0); *T. bradfieldi* (197.0); *T. camurus* (104.0); *T. deckeni* (170.0); *T. erythrorhynchus* (139.0); *T. fasciatus* (260.0); *T. flavirostris* (220.0); *T. hartlaubi* (99.1); *T. hemprichii* (297.0); *T. leucomelas* (190.0); *T. monteiri* (305.0); *T. nasutus* (183.0); *T. pallidirostris* (234.0); *Bucorvus abyssinicus* (4000.0); *B. cafer* (3841.0); *Burhinus bistriatus* (787.0); *B. capensis* (423.0); *B. giganteus* (1025.0); *B. magnirostris* (1016.0); *B. oedicnemus* (459.0); *B. recurvirostris* (790.0); *B. senegalensis* (326.0); *B. superciliaris* (450.0); *B. vermiculatus* (320.0); *Caprimulgus aegyptius* (77.3); *C. affinis* (58.7); *C. anthonyi* (35.9); *C. asiaticus* (42.0); *C. atripennis* (61.0); *C. badius* (59.8); *C. batesi* (100.0); *C. binotatus* (63.0); *C. candicans* (49.3); *C. carolinensis* (109.0); *C. cayennensis* (35.5); *C. centralasicus* (67.0); *C. clarus* (42.5); *C. climacurus* (45.8); *C. donaldsoni* (29.0); *C. europaeus* (67.0); *C. eximius* (66.3); *C. fossii* (58.3); *C. fraenatus* (60.1); *C. hirundinaceus* (19.7); *C. indicus* (91.8); *C. inornatus* (50.4); *C. longirostris* (45.6); *C. macrurus* (66.2); *C. maculicaudus* (30.3); *C. maculosus* (26.4); *C. mahrattensis* (57.0); *C. natalensis* (77.7); *C. nigrescens* (35.7); *C. nigriscapularis* (49.0); *C. nubicus* (49.3); *C. parvulus* (37.0); *C. pectoralis* (52.5); *C. poliocephalus* (41.8); *C. ridgwayi* (48.0); *C. ruficollis* (68.5); *C. rufigena* (52.5); *C. rufus* (94.2); *C. ruwenzorii* (49.0); *C. salvini* (56.0); *C. saturatus* (52.0); *C. sericocaudatus* (83.0); *C. stellatus* (58.2); *C. tristigma* (79.0); *C. vociferus* (53.4); *C. whiteleyi* (41.0); *Chordeiles acutipennis* (48.5); *C. minor* (79.3); *C. pusillus* (33.4); *C. rupestris* (45.2); *C. vielliardi* (24.0); *Eleothreptus anomalus* (43.7); *Hydropsalis climacocerca* (46.0); *H. torquata* (57.8); *Lurocalis rufiventris* (59.3); *L. semitorquatus* (75.9); *Macrodipteryx longipennis* (48.0); *M. vexillar-*

ia (72.4); *Macropsalis forcipata* (120.0); *Nyctidromus albicollis* (58.1); *Nyctiphrynus mcleodii* (35.0); *N. ocellatus* (39.6); *N. rosenbergi* (52.0); *N. yucatanicus* (24.5); *Nyctiprogne leucopyga* (27.3); *Phalaenoptilus nuttallii* (48.4); *Podager nacunda* (159.0); *Uropsalis lyra* (71.2); *U. segmentata* (42.9); *Cariama cristata* (1400.0); *Chunga burmeisteri* (1298.0); *Casuarius casuarius* (44000.0); *Centropus anselli* (210.0); *C. bengalensis* (161.0); *C. cupreicaudus* (286.0); *C. grillii* (226.0); *C. leucogaster* (309.0); *C. monachus* (204.0); *C. phasianinus* (390.0); *C. rectunguis* (238.0); *C. senegalensis* (169.0); *C. sinensis* (283.0); *C. superciliosus* (150.0); *Auriparus flaviceps* (6.8); *Campylorhynchus albobrunneus* (32.9); *C. brunneicapillus* (38.9); *C. chiapensis* (50.9); *C. fasciatus* (30.0); *C. griseus* (42.4); *C. gularis* (30.1); *C. jocosus* (27.6); *C. megalopterus* (33.1); *C. nuchalis* (23.2); *C. rufinucha* (31.0); *C. turdinus* (32.6); *C. yucatanicus* (35.5); *C. zonatus* (34.6); *Catherpes mexicanus* (11.3); *Certhia americana* (8.1); *C. brachydactyla* (8.2); *C. discolor* (10.4); *C. familiaris* (9.0); *C. himalayana* (8.8); *C. nipalensis* (11.1); *Cinnycerthia fulva* (16.6); *C. olivascens* (24.5); *C. peruana* (19.5); *C. unirufa* (29.4); *Cistothorus apolinari* (17.7); *C. meridae* (12.9); *C. palustris* (10.6); *C. platensis* (8.5); *Cyphorhinus arada* (20.9); *C. phaeocephalus* (24.6); *C. thoracicus* (31.4); *Donacobius atricapilla* (36.8); *Henicorhina leucophrys* (15.9); *H. leucoptera* (13.8); *H. leucosticta* (14.2); *Hylorchilus navai* (29.3); *H. sumichrasti* (28.4); *Microbates cinereiventris* (11.9); *M. collaris* (10.2); *Microcerculus bambla* (19.1); *M. marginatus* (18.0); *M. philomela* (17.8); *M. ustulatus* (21.0); *Odontorchilus branickii* (9.6); *O. cinereus* (11.0); *Polioptila albiloris* (6.3); *P. caerulea* (5.8); *P. californica* (5.8); *P. dumicola* (7.0); *P. guianensis* (5.9); *P. lactea* (6.5); *P. maior* (6.5); *P. melanura* (5.2); *P. nigriceps* (5.6); *P. plumbea* (6.1); *P. schistaceigula* (6.0); *Ramphocaenus melanurus* (9.7); *Salpinctes obsoletus* (16.5); *Salpornis spilonotus* (14.8); *Thryomanes bewickii* (9.9); *Thryorchilus browni* (14.0); *Thryothorus atrogularis* (24.3); *T. colombianus* (16.0); *T. coraya* (17.2); *T. eisenmanni* (23.2); *T. euophrys* (30.5); *T. fasciatoventris* (24.0); *T. felix* (13.2); *T. genibarbis* (19.2); *T. griseus* (13.8); *T. guarayanus* (13.5); *T. leucopogon* (15.1); *T. leucotis* (19.5); *T. longirostris* (21.3); *T. ludovicianus* (18.6); *T. maculipectus* (15.1); *T. modestus* (17.1); *T. mystacalis* (29.0); *T. nicefori* (21.9); *T. nigricapillus* (23.9); *T. paucimaculatus* (16.0); *T. pleurostictus* (17.7); *T. rufalbus* (24.3); *T. rutilus* (16.5); *T. sclateri* (20.0); *T. semibadius* (17.0); *T. sinaloa* (15.1); *T. spadix* (21.9); *T. superciliaris* (22.8); *T. thoracicus* (17.6); *Troglodytes aedon* (10.9); *T. monticola* (12.1); *T. ochraceus* (9.5); *T. rufociliatus* (11.0); *T. rufulus* (16.0); *T. solstitialis* (12.5); *T. troglodytes* (9.0); *Uropsila leucogastra* (9.1); *Ceryle rudis* (84.4); *Chloroceryle aenea* (13.8); *C. amazona* (127.0); *C. americana* (34.8); *C. inda* (52.1); *Megaceryle alcyon* (148.0); *M. lugubris* (272.0); *M. maxima* (325.0); *M. torquata* (317.0); *Charadrius alexandrinus* (42.3); *C. alticola* (44.9); *C. asiaticus* (77.1); *C. australis* (79.0); *C. collaris* (28.3); *C. dubius* (38.7); *C. falklandicus* (65.0); *C. forbesi* (47.2); *C. hiaticula* (64.1); *C. leschenaultii* (74.8); *C. marginatus* (48.3); *C. melanops* (30.0); *C. melodus* (54.4); *C. modestus* (78.0); *C. mongolus* (64.0); *C. montanus* (95.8); *C. pallidus* (34.8); *C. pecuarius* (34.0); *C. peronii* (42.0); *C. placidus* (62.7); *C. ruficapillus* (37.4); *C. semipalmatus* (46.8); *C. tricollaris* (31.2); *C. veredus* (95.0); *C. vociferus* (96.6); *Cladorhynchus leucocephalus* (216.0); *Erythrogonys cinctus* (51.4); *Eudromias morinellus* (114.0); *Haematopus moquini* (692.0); *H. ostralegus* (526.0); *Himantopus himantopus* (161.0); *H. melanurus* (218.0); *H. mexicanus* (202.0); *Hoplopterus spinosus* (100.0); *Hoploxypterus cayanus* (74.0); *Ibidorhyncha struthersi* (294.0); *Oreopholus ruficollis* (131.0); *Phegornis mitchellii* (35.5); *Pluvialis apricaria* (214.0); *P. dominica* (151.5); *P. fulva* (135.0); *P. squatarola* (250.0); *Recurvirostra americana* (304.5); *R. andina* (361.0); *R. avosetta* (304.0); *R. novaehollandiae* (325.0); *Thinornis rubricollis* (100.0); *Vanellus albiceps* (192.0); *V. armatus* (156.0); *V. chilensis* (327.0); *V. cinereus* (270.0); *V. coronatus* (165.0); *V. crassirostris* (170.0); *V. duvaucelii* (158.8); *V. gregarius* (226.0); *V. indicus* (181.0); *V. leucurus* (132.0); *V. lugubris* (122.0); *V. malabaricus* (140.0); *V. melanocephalus* (214.0); *V. melanopterus* (185.0); *V. miles* (387.0); *V. resplendens* (214.0); *V. senegallus* (248.0); *V. superciliosus* (150.0); *V. tectus* (100.0); *V. tricolor* (184.0); *V. vanellus* (218.5); *Anastomus lamelligerus* (1081.0); *A. oscitans* (808.0); *Cathartes aura* (1552.0); *C. burrovianus* (935.0); *C. melambrotus* (1373.0); *Ciconia abdimii* (1398.0); *C. boyciana* (5351.0); *C. ciconia* (3448.0); *C. episcopus* (2061.0); *C. maguari* (4000.0); *C. nigra* (2926.0); *C. stormi* (3018.0); *Coragyps atratus* (1900.0); *Ephippiorhynchus asiaticus* (4100.0); *E. senegalensis* (6163.0); *Gymnogyps californianus* (8450.0); *Jabiru mycteria* (6055.0); *Leptoptilos crumeniferus* (6325.0); *L. dubius* (5500.0); *L. javanicus* (4651.0); *Mycteria americana* (2559.0); *M. cinerea* (2000.0); *M. ibis* (2167.0); *M. leucocephala* (3180.0); *Sarcoramphus papa* (3400.0); *Vultur gryphus* (11300.0); *Cinclus cinclus* (61.7); *C. leucocephalus* (44.0); *C. mexicanus* (56.8); *C. pallasii* (76.0); *C. schulzi* (37.6); *Apalis alticola* (12.1); *A. bamendae* (8.5); *A. binotata* (8.2); *A. chapini* (8.8); *A. chariessa* (8.5); *A. chirindensis* (8.6); *A. cinerea* (9.9); *A. flavida* (8.2); *A. goslingi* (8.2); *A. jacksoni* (8.7); *A. karamojae* (9.2); *A. melanocephala* (8.8); *A. nigriceps* (8.4); *A. personata* (11.0); *A. por-*

phyrolaema (8.4); *A. pulchra* (8.4); *A. ruddi* (9.7); *A. rufogularis* (8.4); *A. ruwenzorii* (9.9); *A. sharpii* (8.7); *A. thoracica* (11.3); *Artisornis metopias* (8.0); *A. moreaui* (8.0); *Calamonastes fasciolastus* (13.1); *C. simplex* (13.0); *C. undosus* (13.0); *Camaroptera brachyura* (10.0); *C. chloronota* (11.4); *C. superciliaris* (9.7); *Cisticola aberdare* (24.0); *C. aberrrans* (14.2); *C. angusticaudus* (10.0); *C. anonymus* (14.0); *C. aridulus* (9.3); *C. ayresii* (7.0); *C. bodessa* (17.5); *C. brachypterus* (7.9); *C. brunnescens* (8.0); *C. bulliens* (15.9); *C. cantans* (11.7); *C. carruthersi* (11.3); *C. chiniana* (10.0); *C. chubbi* (16.1); *C. cinereolus* (17.2); *C. cinnamomeus* (9.0); *C. dambo* (9.0); *C. dorsti* (13.0); *C. erythrops* (13.0); *C. exilis* (7.1); *C. eximius* (12.0); *C. fulvicapillus* (8.3); *C. galactotes* (12.8); *C. hunteri* (15.5); *C. juncidis* (6.9); *C. lais* (14.9); *C. lateralis* (16.9); *C. melanurus* (8.8); *C. nanus* (5.0); *C. natalensis* (16.9); *C. nigriloris* (19.8); *C. njombe* (10.9); *C. pipiens* (13.5); *C. restrictus* (13.2); *C. robustus* (19.5); *C. ruficeps* (9.7); *C. rufilatus* (11.3); *C. rufus* (7.3); *C. subruficapillus* (10.0); *C. textrix* (10.5); *C. tinniens* (12.9); *C. troglodytes* (9.0); *C. woosnami* (13.5); *Drymocichla incana* (10.0); *Eminia lepida* (20.2); *Euryptila subcinnamonea* (11.5); *Heliolais erythroptera* (12.7); *Hypergerus atriceps* (29.8); *Malcorus pectoralis* (10.2); *Oreophilais robertsi* (8.9); *Phragmacia substriata* (12.4); *Prinia atrogularis* (11.8); *P. bairdii* (13.4); *P. buchanani* (7.0); *P. burnesii* (12.0); *P. cinereocapilla* (6.8); *P. criniger* (13.8); *P. flavicans* (8.8); *P. flaviventris* (7.0); *P. fluviatilis* (9.0); *P. gracilis* (7.1); *P. hodgsonii* (6.4); *P. inornata* (7.0); *P. maculosa* (9.0); *P. polychroa* (11.0); *P. rufescens* (6.5); *P. socialis* (8.0); *P. somalica* (7.5); *P. subflava* (8.7); *P. sylvatica* (16.1); *Rhopophilus pekinensis* (18.1); *Scotocerca inquieta* (8.2); *Spiloptila clamans* (7.0); *Urolais epichlora* (11.3); *Climacteris affinis* (21.7); *C. erythrops* (23.3); *C. melanura* (31.9); *C. picumnus* (30.7); *C. rufa* (32.7); *Cormobates leucophaeus* (22.0); *Coccyzus americanus* (64.0); *C. cinereus* (41.3); *C. erythropthalmus* (50.9); *C. euleri* (52.3); *C. lansbergi* (50.3); *C. melacoryphus* (49.9); *C. minor* (63.9); *C. pumilus* (37.1); *Piaya cayana* (102.0); *P. melanogaster* (100.0); *P. minuta* (40.0); *Colius castanotus* (60.5); *C. colius* (41.4); *C. striatus* (51.1); *Urocolius indicus* (81.4); *U. macrourus* (45.5); *Chalcophaps indica* (138.0); *Claravis godefrida* (68.1); *C. mondetoura* (89.7); *C. pretiosa* (68.2); *Columba albinucha* (285.0); *C. albitorques* (277.0); *C. araucana* (363.7); *C. arquatrix* (400.0); *C. cayennensis* (250.0); *C. corensis* (284.9); *C. delegorguei* (133.0); *C. elphinstonii* (379.0); *C. eversmanni* (202.0); *C. fasciata* (398.0); *C. flavirostris* (324.0); *C. goodsoni* (206.2); *C. guinea* (352.0); *C. hodgsonii* (377.6); *C. iriditorques* (126.0); *C. janthina* (397.0); *C. larvata* (155.0); *C. leucocephala* (240.0); *C. leucomela* (410.0); *C. leuconota* (285.0); *C. livia* (355.0); *C. maculosa* (347.0); *C. nigrirostris* (150.0); *C. oenas* (291.0); *C. oenops* (223.7); *C. oliviae* (367.9); *C. palumbus* (490.0); *C. picazuro* (402.0); *C. plumbea* (207.0); *C. pulchricollis* (330.0); *C. punicea* (440.0); *C. rupestris* (296.0); *C. sjostedti* (367.9); *C. speciosa* (320.0); *C. subvinacea* (170.0); *C. unicincta* (391.0); *Columbina buckleyi* (57.5); *C. cruziana* (50.1); *C. cyanopis* (30.8); *C. minuta* (32.6); *C. passerina* (37.0); *C. picui* (47.0); *C. talpacoti* (45.6); *Ducula aenea* (545.0); *D. badia* (486.0); *D. bicolor* (410.0); *D. spilorrhora* (456.0); *Geopelia cuneata* (31.6); *G. humeralis* (129.0); *G. striata* (56.6); *Geophaps plumifera* (94.6); *G. scripta* (222.0); *G. smithii* (194.0); *Geotrygon albifacies* (238.0); *G. carrikeri* (267.0); *G. chiriquensis* (308.0); *G. costaricensis* (287.0); *G. frenata* (307.0); *G. goldmani* (258.0); *G. lawrencii* (220.0); *G. linearis* (261.0); *G. montana* (115.0); *G. purpurata* (159.4); *G. saphirina* (203.0); *G. veraguensis* (155.0); *G. violacea* (95.2); *Leptotila battyi* (161.0); *L. cassini* (159.0); *L. conoveri* (164.1); *L. jamaicensis* (165.0); *L. megalura* (218.0); *L. ochraceiventris* (146.0); *L. pallida* (127.0); *L. plumbeiceps* (170.0); *L. rufaxilla* (157.0); *L. verreauxi* (148.0); *Leucosarcia melanoleuca* (429.0); *Macropygia amboinensis* (237.0); *M. ruficeps* (258.0); *M. unchall* (200.0); *Metriopelia aymara* (61.8); *M. ceciliae* (55.1); *M. melanoptera* (100.0); *M. morenoi* (49.2); *Ocyphaps lophotes* (220.0); *Oena capensis* (40.6); *Ptilinopus jambu* (135.0); *P. magnificus* (360.0); *P. regina* (115.0); *P. superbus* (118.0); *Scardafella inca* (48.0); *S. squammata* (54.0); *Streptopelia capicola* (142.0); *S. chinensis* (159.0); *S. decaocto* (149.0); *S. decipiens* (134.0); *S. hypopyrrha* (162.0); *S. lugens* (155.0); *S. orientalis* (233.0); *S. reichenowi* (119.0); *S. roseogrisea* (155.0); *S. semitorquata* (176.0); *S. senegalensis* (83.9); *S. tranquebarica* (103.0); *S. turtur* (132.0); *S. vinacea* (110.0); *Treron apicauda* (220.0); *T. bicincta* (170.0); *T. calva* (210.0); *T. capellei* (397.0); *T. curvirostra* (149.0); *T. olax* (77.0); *T. phoenicoptera* (261.0); *T. pompadora* (151.0); *T. seimundi* (130.0); *T. sieboldii* (238.0); *T. sphenura* (213.0); *T. vernans* (132.5); *T. waalia* (268.0); *Turtur abyssinicus* (62.7); *T. afer* (65.6); *T. brehmeri* (116.0); *T. chalcospilos* (60.6); *T. tympanistria* (70.7); *Uropelia campestris* (35.2); *Zenaida asiatica* (153.0); *Z. auriculata* (26.0); *Z. aurita* (156.0); *Z. macroura* (123.0); *Z. meloda* (210.0); *Conopophaga ardesiaca* (26.3); *C. aurita* (25.5); *C. castaneiceps* (27.0); *C. cearae* (22.1); *C. lineata* (25.6); *C. melanogaster* (42.5); *C. melanops* (20.1); *C. peruviana* (23.0); *C. roberti* (20.8); *Coracias abyssinica* (102.0); *C. benghalensis* (158.0); *C. caudata* (110.0); *C. cyanogaster* (142.0); *C. garrulus* (146.0); *C. naevia* (168.0); *C. spatulata* (93.0); *Eurystomus glaucurus* (110.0); *E. gularis* (96.3); *E. orientalis* (129.0);

Aegithina lafresnayei (14.7); *A. nigrolutea* (12.0); *A. tiphia* (12.0); *A. viridissima* (13.4); *Antichromus minutus* (33.8); *Aphelocoma californica* (86.1); *A. coerulescens* (77.2); *A. ultramarina* (115.0); *A. unicolor* (124.0); *Arses kaupi* (13.5); *A. telescophthalmus* (13.7); *Artamus cinereus* (35.6); *A. cyanopterus* (34.6); *A. fuscus* (39.8); *A. leucorynchus* (41.7); *A. minor* (16.0); *A. personatus* (34.6); *A. superciliosus* (35.5); *Batis capensis* (11.6); *B. diops* (12.7); *B. fratrum* (12.0); *B. ituriensis* (10.0); *B. margaritae* (11.7); *B. minima* (10.0); *B. minor* (12.5); *B. minulla* (9.9); *B. mixta* (12.2); *B. molitor* (11.7); *B. orientalis* (11.1); *B. perkeo* (7.0); *B. poensis* (9.6); *B. pririt* (9.4); *B. senegalensis* (9.7); *B. soror* (9.5); *Bias musicus* (21.9); *Calocitta colliei* (234.0); *C. formosa* (210.0); *Campephaga flava* (32.3); *C. petiti* (31.4); *C. phoenicea* (27.1); *C. quiscalina* (34.5); *Cinclosoma castaneothorax* (65.0); *C. castanotus* (64.3); *C. cinnamomeum* (56.2); *C. punctatum* (113.5); *Cissam (or Urocissa) chinensis* (127.0); *C. hypoleuca* (120.0); *Colluricincla boweri* (43.8); *C. harmonica* (66.0); *C. megarhyncha* (32.4); *C. woodwardi* (54.5); *Coracina azurea* (47.0); *C. caesia* (42.8); *C. fimbriata* (29.3); *C. graueri* (69.0); *C. lineata* (69.3); *C. macei* (100.0); *C. maxima* (140.0); *C. melanoptera* (30.0); *C. melaschistos* (38.5); *C. novaehollandiae* (104.0); *C. papuensis* (78.5); *C. pectoralis* (58.0); *C. polioptera* (35.8); *C. striata* (111.0); *C. tenuirostris* (61.0); *Corcorax melanorhamphos* (364.0); *Corvus albicollis* (894.0); *C. albus* (524.0); *C. bennetti* (389.0); *C. brachyrhynchos* (453.0); *C. capensis* (553.0); *C. caurinus* (392.0); *C. corax* (941.0); *C. corone* (570.0); *C. coronoides* (645.0); *C. crassirostris* (1135.0); *C. cryptoleucus* (534.0); *C. dauuricus* (208.0); *C. edithae* (442.0); *C. enca* (251.0); *C. frugilegus* (454.0); *C. imparatus* (221.0); *C. levaillantii* (365.0); *C. macrorhynchos* (520.0); *C. mellori* (541.0); *C. monedula* (279.0); *C. orru* (492.0); *C. ossifragus* (285.0); *C. rhipidurus* (611.0); *C. ruficollis* (559.0); *C. sinaloae* (244.0); *C. spendens* (294.0); *C. tasmanicus* (678.0); *C. torquatus* (471.0); *Cracticus mentalis* (31.6); *C. nigrogularis* (128.0); *C. quoyi* (168.0); *C. torquatus* (83.1); *Crypsirina cucullata* (76.8); *C. temia* (83.1); *Cyanocitta cristata* (88.0); *C. stelleri* (128.0); *Cyanocorax affinis* (212.0); *C. beecheii* (193.0); *C. caeruleus* (272.0); *C. cayanus* (175.0); *C. chrysops* (166.0); *C. cristatellus* (178.0); *C. cyanomelas* (207.0); *C. cyanopogon* (146.0); *C. dickeyi* (181.0); *C. heilprini* (178.2); *C. luxuosus* (100.0); *C. melanocyaneus* (101.0); *C. morio* (204.0); *C. mystacalis* (155.0); *C. sanblasianus* (109.0); *C. violaceus* (262.0); *C. yncas* (78.5); *C. yucatanicus* (118.0); *Cyanolyca argentigula* (200.0); *C. armillata* (200.0); *C. cucullata* (102.0); *C. mirabilis* (52.4); *C. nana* (41.0); *C. pulchra* (65.6); *C. pumilo* (47.0); *C. turcosa* (83.1); *C. viridicyana* (120.0); *Cyanopica cyana* (96.0); *Daphoenositta chrysoptera* (11.7); *Dendrocitta formosae* (103.0); *D. frontalis* (90.0); *D. leucogastra* (99.2); *D. vagabunda* (100.0); *Dicrurus adsimilis* (40.3); *D. aeneus* (26.5); *D. annectans* (44.0); *D. atripennis* (38.9); *D. bracteatus* (85.7); *D. caerulescens* (40.0); *D. hottentottus* (79.2); *D. leucophaeus* (37.6); *D. ludwigii* (29.4); *D. macrocercus* (48.3); *D. modestus* (45.6); *D. paradiseus* (131.3); *D. remifer* (43.1); *Dryoscopus angolensis* (36.0); *D. cubla* (26.3); *D. gambensis* (31.9); *D. pringlii* (19.7); *D. sabini* (37.2); *D. senegalensis* (29.3); *Dyaphorophyia blissetti* (10.0); *D. castanea* (11.0); *D. concreta* (10.0); *D. tonsa* (10.5); *Elminia albicauda* (8.4); *E. albiventris* (8.9); *E. albonotata* (9.2); *E. longicauda* (9.9); *E. nigromitrata* (9.1); *Erythrocercus holochlorus* (6.0); *E. livingstonei* (5.9); *E. mccallii* (7.2); *Eupetes macrocerus* (73.1); *Falcunculus frontatus* (28.1); *Garrulus glandarius* (160.0); *G. lanceolatus* (97.7); *Grallina cyanoleuca* (86.5); *Gymnorhina tibicen* (287.0); *Gymnorhinus cyanocephalus* (105.0); *Hemipus picatus* (9.0); *Hypothymis azurea* (10.2); *Lalage leucomela* (29.4); *L. nigra* (28.4); *L. sueurii* (18.9); *Laniarius aethiopicus* (49.5); *L. amboimensis* (49.0); *L. atrococcineus* (48.8); *L. atroflavus* (43.0); *L. barbarus* (47.1); *L. bicolor* (49.0); *L. erythrogaster* (48.8); *L. ferrugineus* (46.8); *L. fuelleborni* (46.4); *L. funebris* (40.4); *L. leucorhynchus* (50.3); *L. liberatus* (44.8); *L. luehderi* (42.9); *L. mufumbiri* (41.5); *L. poensis* (44.9); *L. ruficeps* (32.8); *L. turatii* (49.0); *Lanioturdus torquatus* (29.0); *Lobotos lobatus* (63.0); *L. oriolinus* (58.0); *Machaerirhynchus flaviventer* (9.7); *Malaconotus alius* (73.0); *M. blanchoti* (78.7); *M. bocagei* (52.4); *M. cruentus* (76.7); *M. gladiator* (99.0); *M. kupeensis* (60.3); *M. lagdeni* (92.3); *M. monteiri* (79.4); *M. multicolor* (52.4); *M. nigrifrons* (32.4); *M. olivaceus* (33.6); *M. sulfureopectus* (30.8); *Manucodia keraudrenii* (156.0); *Megabyas flammulatus* (28.1); *Monarcha frater* (22.0); *M. leucotis* (11.4); *M. melanopsis* (22.7); *M. trivirgatus* (12.7); *Myiagra alecto* (19.6); *M. cyanoleuca* (17.5); *M. inquieta* (20.9); *M. rubecula* (11.9); *M. ruficollis* (10.1); *Nilaus afer* (19.4); *Nucifraga caryocatactes* (178.0); *N. columbiana* (130.0); *Oreoica gutturalis* (62.9); *Oriolus auratus* (73.7); *O. brachyrhynchus* (49.2); *O. chinensis* (85.7); *O. chlorocephalus* (65.0); *O. flavocinctus* (75.5); *O. larvatus* (63.5); *O. mellianus* (71.3); *O. monacha* (65.7); *O. nigripennis* (54.7); *O. oriolus* (71.6); *O. percivali* (82.3); *O. sagittatus* (98.0); *O. tenuirostris* (75.5); *O. traillii* (67.5); *O. xanthonotus* (45.0); *O. xanthornus* (56.7); *Pachycephala grisola* (21.0); *P. inornata* (30.8); *P. lanioides* (38.8); *P. melanura* (23.8); *P. olivacea* (41.2); *P. pectoralis* (26.3); *P. rufiventris* (22.6); *P. rufogularis* (36.6); *P. simplex* (23.3); *Pericrocotus brevirostris* (16.5); *P. cantonensis* (24.0); *P. cinnamomeus* (8.6); *P. divaricatus* (24.6);

P. erythropygius (10.8); *P. ethologus* (19.0); *P. flammeus* (23.3); *P. igneus* (15.0); *P. roseus* (17.2); *P. solaris* (14.5); *Perisoreus canadensis* (71.7); *P. infaustus* (84.4); *P. internigrans* (102.0); *Philentoma pyrhopterum* (16.9); *P. velatum* (26.1); *Pica nuttalli* (159.0); *P. pica* (206.0); *Platylophus galericulatus* (77.9); *Platysmurus leucopterus* (180.0); *Platysteira albifrons* (12.2); *P. cyanea* (14.6); *P. peltata* (13.7); *Podoces biddulphi* (110.0); *P. hendersoni* (121.0); *P. panderi* (91.1); *P. pleskei* (87.5); *Prionops alberti* (61.3); *P. caniceps* (50.3); *P. gabela* (39.7); *P. plumatus* (33.8); *P. poliolophus* (49.0); *P. retzii* (49.6); *P. rufiventris* (40.6); *P. scopifrons* (29.4); *Pseudopodoces humilis* (45.5); *Psophodes cristatus* (40.8); *P. nigrogularis* (44.6); *P. occidentalis* (39.8); *P. olivaceus* (62.6); *Ptiloris magnificus* (154.0); *P. paradiseus* (121.0); *P. victoriae* (95.5); *Ptilostomus afer* (128.0); *Pyrrhocorax graculus* (212.0); *P. pyrrhocorax* (278.0); *Rhipidura albicollis* (11.5); *R. aureola* (10.0); *R. fuliginosa* (13.9); *R. hypoxantha* (5.5); *R. javanica* (12.5); *R. leucophrys* (29.5); *R. perlata* (13.4); *R. phasiana* (7.0); *R. rufifrons* (10.2); *R. rufiventris* (15.0); *Sphecotheres viridis* (121.5); *Strepera graculina* (299.5); *S. versicolor* (396.5); *Struthidea cinerea* (132.0); *Tchagra australis* (32.3); *T. jamesi* (27.4); *T. senegala* (53.5); *T. tchagra* (50.3); *Telophorus cruentus* (54.0); *T. dohertyi* (35.3); *T. viridis* (37.2); *T. zeylonus* (66.1); *Temnurus temnurus* (78.1); *Tephrodornis gularis* (37.8); *T. pondicerianus* (20.2); *Terpsiphone batesi* (15.2); *T. bedfordi* (12.1); *T. paradisi* (19.3); *T. rufiventer* (15.1); *T. rufocinerea* (15.4); *T. viridis* (13.3); *Trochocercus cyanomelas* (10.2); *T. nitens* (11.8); *Urocissa erythrorhyncha* (152.0); *U. flavirostris* (151.0); *U. whiteheadi* (106.5); *Zavattariornis stresemanni* (75.6); *Aburria aburri* (1408.0); *Chamaepetes goudotii* (729.0); *C. unicolor* (1135.0); *Crax alberti* (2800.0); *C. alector* (3086.0); *C. blumenbachii* (3500.0); *C. daubentoni* (2507.0); *C. fasciolata* (2600.0); *C. globulosa* (2500.0); *C. rubra* (4133.0); *Mitu mitu* (2853.0); *M. salvini* (2100.0); *M. tomentosa* (2200.0); *M. tuberosa* (2813.0); *Nothocrax urumutum* (1700.0); *Oreophasis derbianus* (2076.0); *Ortalis araucuan* (550.0); *O. canicollis* (539.0); *O. cinereiceps* (493.0); *O. columbiana* (500.0); *O. erythroptera* (632.0); *O. garrula* (534.0); *O. guttata* (550.0); *O. leucogastra* (500.0); *O. motmot* (520.0); *O. poliocephala* (760.0); *O. ruficauda* (589.0); *O. ruficeps* (473.8); *O. squamata* (550.0); *O. superciliaris* (850.0); *O. vetula* (563.0); *O. wagleri* (834.0); *Pauxi pauxi* (3150.0); *P. unicornis* (3745.0); *Penelope albipennis* (1750.0); *P. argyrotis* (808.0); *P. barbata* (807.5); *P. dabbenei* (1230.0); *P. jacquacu* (1490.0); *P. jacucaca* (1282.0); *P. marail* (880.0); *P. montagnii* (706.0); *P. obscura* (1770.0); *P. ochrogaster* (1084.8); *P. ortoni* (1016.5); *P. perspicax* (1234.9); *P. pileata* (2150.0); *P. purpurascens* (2060.0); *P. superciliaris* (895.0); *Penelopina nigra* (890.0); *Pipile jacutinga* (1250.0); *P. pipile* (2150.0); *Crotophaga ani* (111.0); *C. major* (149.0); *C. sulcirostris* (82.2); *Guira guira* (141.0); *Cacomantis castaneiventris* (34.9); *C. flabelliformis* (49.9); *C. merulinus* (26.0); *C. passerinus* (26.0); *C. sepulcralis* (33.4); *C. sonneratii* (32.0); *C. variolosus* (14.1); *Carpococcyx renauldi* (400.0); *Cercococcyx mechowi* (56.5); *C. montanus* (49.5); *C. olivinus* (65.0); *Ceuthmochares aereus* (65.8); *Chrysococcyx basalis* (23.2); *C. caprius* (33.0); *C. cupreus* (37.7); *C. flavigularis* (23.1); *C. klaas* (27.4); *C. lucidus* (24.5); *C. maculatus* (27.5); *C. minutillus* (18.6); *C. osculans* (30.9); *C. russatus* (18.6); *C. xanthorhynchus* (22.6); *Clamator coromandus* (75.1); *C. glandarius* (134.0); *Cuculus canorus* (112.0); *C. clamosus* (79.5); *C. crassirostris* (80.0); *C. fugax* (79.7); *C. gularis* (103.0); *C. micropterus* (95.1); *C. pallidus* (87.7); *C. poliocephalus* (47.1); *C. rochii* (62.7); *C. saturatus* (81.1); *C. solitarius* (78.0); *C. sparverioides* (151.0); *C. vagans* (57.7); *C. varius* (103.0); *Eudynamys scolopacea* (194.0); *Oxylophus jacobinus* (72.4); *O. levaillantii* (122.0); *Pachycoccyx audeberti* (104.0); *Phaenicophaeus chlorophaeus* (51.3); *P. curvirostris* (154.0); *P. diardi* (62.1); *P. javanicus* (109.0); *P. leschenaultii* (179.0); *P. sumatranus* (92.2); *P. tristis* (117.0); *P. viridirostris* (67.0); *Scythrops novaehollandiae* (630.0); *Surniculus lugubris* (29.7); *Actenoides concretus* (73.5); *Dacelo leachii* (309.0); *D. novaeguineae* (335.0); *Halcyon albiventris* (65.1); *H. badia* (57.9); *H. chelicuti* (44.5); *H. coromanda* (77.5); *H. leucocephala* (41.8); *H. malimbica* (91.8); *H. pileata* (84.0); *H. senegalensis* (74.5); *H. senegaloides* (61.8); *H. smyrnensis* (91.4); *Lacedo pulchella* (47.6); *Pelargopsis amauropterus* (162.0); *P. capensis* (181.0); *Syma torotoro* (37.7); *Tanysiptera sylvia* (49.6); *Todirhamphus chloris* (68.1); *T. macleayii* (37.3); *T. pyrrhopygia* (51.7); *T. sanctus* (54.1); *Dendrocygna arcuata* (730.0); *D. autumnalis* (756.0); *D. bicolor* (757.0); *D. eytoni* (790.0); *D. javanica* (525.0); *D. viduata* (690.0); *Thalassornis leuconotus* (708.0); *Culicicapa ceylonensis* (8.0); *Drymodes brunneopygia* (33.2); *D. superciliaris* (45.9); *Eopsaltria australis* (20.3); *E. georgiana* (19.2); *E. griseogularis* (19.4); *E. pulverulenta* (19.3); *Heteromyias albispecularis* (36.3); *Melanodryas cucullata* (21.3); *Microeca fascinans* (14.6); *M. flavigaster* (12.3); *M. griseoceps* (10.6); *M. tormentii* (11.8); *Petroica goodenovii* (8.9); *P. multicolor* (12.5); *P. phoenicea* (13.0); *P. rodinogaster* (10.3); *P. rosea* (8.2); *Poecilodryas superciliosa* (19.9); *Tregellasia capito* (13.9); *T. leucops* (14.9); *Eurostopodus argus* (93.4); *E. macrotis* (141.0); *E. mystacalis* (139.0); *E. temminckii* (95.9); *Calyptomena viridis* (58.5); *Corydon sumatranus* (31.1); *Cymbirhynchus macrorhynchos* (59.4); *Eurylaimus javanicus* (78.2); *E. ochromalus*

(33.3); *Psarisomus dalhousiae* (67.0); *Pseudocalyptomena graueri* (31.8); *Serilophus lunatus* (34.0); *Smithornis capenis* (23.2); *S. rufolateralis* (19.1); *S. sharpei* (37.5); *Eurypyga helias* (210.0); *Caracara cheriway* (1032.0); *C. plancus* (1348.0); *Daptrius ater* (352.0); *Falco alopex* (225.0); *F. amurensis* (142.0); *F. ardosiaceus* (235.0); *F. berigora* (594.0); *F. biarmicus* (616.0); *F. cenchroides* (170.0); *F. cherrug* (966.0); *F. chicquera* (208.0); *F. columbarius* (191.0); *F. concolor* (250.0); *F. cuvieri* (183.0); *F. deiroleucus* (481.0); *F. dickinsoni* (209.0); *F. eleonorae* (390.0); *F. fasciinucha* (259.0); *F. femoralis* (344.0); *F. hypoleucos* (480.0); *F. jugger* (755.0); *F. longipennis* (253.0); *F. mexicanus* (734.0); *F. naumanni* (153.0); *F. pelegrinoides* (610.0); *F. peregrinus* (743.0); *F. rufigularis* (168.0); *F. rupicoloides* (261.0); *F. rusticolus* (1461.0); *F. severus* (202.0); *F. sparverius* (121.0); *F. subbuteo* (210.0); *F. subniger* (786.0); *F. tinnunculus* (184.0); *F. vespertinus* (153.0); *Herpetotheres cachinnans* (625.0); *Ibycter americanus* (624.0); *Micrastur buckleyi* (613.5); *M. gilvicollis* (209.0); *M. mirandollei* (549.0); *M. plumbeus* (186.0); *M. ruficollis* (179.0); *M. semitorquatus* (631.0); *Microhierax caerulescens* (40.0); *M. fringillarius* (42.9); *M. melanoleucus* (65.0); *Milvago chimachima* (316.0); *M. chimango* (296.0); *Phalcoboenus albogularis* (809.0); *P. carunculatus* (881.3); *P. megalopterus* (788.0); *Polihierax insignis* (98.0); *P. semitorquatus* (61.5); *Spiziapteryx circumcinctus* (169.0); *Chamaeza campanisona* (99.7); *C. meruloides* (69.0); *C. mollissima* (72.0); *C. nobilis* (123.0); *C. ruficauda* (71.2); *C. turdina* (70.9); *Formicarius analis* (62.2); *F. colma* (47.0); *F. hoffmanni* (59.5); *F. moniliger* (62.2); *F. nigricapillus* (56.2); *F. rufifrons* (55.5); *F. rufipectus* (74.4); *Grallaria albigula* (95.0); *G. alleni* (70.5); *G. andicola* (57.0); *G. bangsi* (62.0); *G. blakei* (42.5); *G. capitalis* (73.7); *G. carrikeri* (110.0); *G. chthonia* (91.0); *G. dignissima* (110.0); *G. eludens* (115.0); *G. erythroleuca* (80.0); *G. erythrotis* (57.0); *G. excelsa* (242.0); *G. flavotincta* (63.0); *G. gigantea* (236.0); *G. griseonucha* (87.4); *G. guatimalensis* (94.2); *G. haplonota* (85.0); *G. hypoleuca* (73.7); *G. kaestneri* (47.5); *G. milleri* (52.5); *G. nuchalis* (117.0); *G. przewalskii* (65.2); *G. quitensis* (65.7); *G. ridgelyi* (180.0); *G. ruficapilla* (80.6); *G. rufocinerea* (44.8); *G. rufula* (35.7); *G. squamigera* (136.0); *G. varia* (119.0); *G. watkinsi* (71.0); *Grallaricula cucullata* (18.7); *G. ferrugineipectus* (17.2); *G. flavirostris* (17.7); *G. leymebambae* (16.6); *G. lineifrons* (21.1); *G. loricata* (20.7); *G. nana* (19.8); *G. ochraceifrons* (23.2); *G. peruviana* (18.8); *Hylopezus auricularis* (40.5); *H. berlepschi* (48.0); *H. dives* (44.0); *H. fulviventris* (41.0); *H. macularius* (44.2); *H. nattereri* (32.0); *H. ochroleucus* (28.0); *H. perspicillatus* (43.0); *Myrmothera campanisona* (47.0); *M. simplex* (52.4); *Pittasoma michleri* (109.0); *P. rufopileatum* (96.5); *Peucedramus taeniatus* (11.0); *Acanthidops bairdii* (16.0); *Agelaioides badius* (22.1); *A. oreopsar* (59.8); *Agelaius cyanopus* (37.6); *A. icterocephalus* (31.0); *A. phoeniceus* (52.4); *A. ruficapillus* (36.8); *A. thilius* (31.7); *A. tricolor* (58.7); *Aimophila aestivalis* (19.6); *A. botterii* (19.9); *A. carpalis* (15.3); *A. cassinii* (18.9); *A. humeralis* (23.9); *A. mystacalis* (22.2); *A. notosticta* (27.1); *A. quinquestriata* (19.6); *A. rufescens* (34.3); *A. ruficauda* (28.2); *A. ruficeps* (19.0); *A. stolzmanni* (25.7); *A. strigiceps* (22.2); *A. sumichrasti* (29.5); *Alario alario* (11.8); *A. leucolaemus* (12.0); *Amaurospiza concolor* (13.1); *A. moesta* (13.6); *Amblycercus holosericeus* (67.3); *Amblyramphus holosericeus* (57.4); *Ammodramus aurifrons* (17.8); *A. bairdii* (18.0); *A. caudacutus* (19.3); *A. henslowii* (12.8); *A. humeralis* (16.0); *A. leconteii* (13.0); *A. maritimus* (22.3); *A. nelsoni* (15.6); *A. savannarum* (18.0); *Amphispiza belli* (16.6); *A. bilineata* (13.5); *Anisognathus flavinuchus* (42.0); *A. igniventris* (34.0); *A. lacrymosus* (31.0); *A. melanogenys* (41.0); *A. notabilis* (39.0); *A. somptuosus* (42.0); *Arremon abeillei* (25.9); *A. aurantiirostris* (34.5); *A. flavirostris* (26.5); *A. franciscanus* (24.9); *A. schlegeli* (27.7); *A. semitorquatus* (24.8); *A. taciturnus* (24.8); *Arremonops chloronotus* (27.4); *A. conirostris* (34.6); *A. rufivirgatus* (22.5); *A. tocuyensis* (18.6); *Atlapetes albiceps* (23.9); *A. albinucha* (33.9); *A. albofrenatus* (30.0); *A. canigenis* (37.6); *A. citrinellus* (28.0); *A. flaviceps* (28.4); *A. forbesi* (37.6); *A. fulviceps* (28.2); *A. fuscoolivaceus* (32.5); *A. gutturalis* (33.0); *A. latinuchus* (30.0); *A. leucopis* (33.0); *A. leucopterus* (20.8); *A. melanocephalus* (28.4); *A. melanolaemus* (25.0); *A. melanops* (23.9); *A. nationi* (41.6); *A. pallidiceps* (23.9); *A. pallidinucha* (34.6); *A. personatus* (32.7); *A. pileatus* (24.0); *A. rufigenis* (37.6); *A. rufinucha* (21.6); *A. schistaceus* (28.1); *A. seebohmi* (26.1); *A. semirufus* (30.7); *A. terborghi* (33.0); *A. tricolor* (36.5); *Bangsia arcaei* (37.2); *B. aureocincta* (41.7); *B. edwardsi* (37.0); *B. melanochlamys* (37.2); *B. rothschildi* (29.6); *Basileuterus basilicus* (14.2); *B. belli* (10.4); *B. bivittatus* (14.6); *B. chlorophrys* (10.7); *B. chrysogaster* (11.2); *B. cinereicollis* (13.1); *B. conspicillatus* (13.1); *B. coronatus* (16.3); *B. culicivorus* (10.5); *B. delatrii* (11.3); *B. flaveolus* (13.2); *B. fraseri* (11.6); *B. fulvicauda* (14.9); *B. griseiceps* (13.1); *B. hypoleucus* (11.4); *B. ignotus* (11.0); *B. leucoblepharus* (15.1); *B. leucophrys* (18.1); *B. luteoviridis* (13.0); *B. melanogenys* (11.8); *B. nigrocristatus* (13.7); *B. rivularis* (13.5); *B. roraimae* (14.5); *B. rufifrons* (10.4); *B. signatus* (11.3); *B. trifasciatus* (9.7); *B. tristriatus* (12.1); *Buarremon atricapillus* (34.9); *B. brunneinuchus* (44.1); *B. torquatus* (42.7); *B. virenticeps* (41.0); *Buthraupis aureodorsalis* (85.0); *B. eximia* (62.7); *B. montana* (87.5); *B. wetmorei* (62.5); *Cacicus cela* (87.5); *C.*

chrysonotus (93.5); *C. chrysopterus* (36.5); *C. haemorrhous* (85.4); *C. koepckeae* (58.5); *C. leucoramphus* (93.5); *C. melanicterus* (82.3); *C. microrhynchus* (60.5); *C. sclateri* (49.0); *C. solitarius* (80.1); *C. uropygialis* (61.7); *Calamospiza melanocorys* (37.6); *Calcarius lapponicus* (27.9); *C. mccownii* (25.7); *C. ornatus* (20.3); *C. pictus* (26.7); *Callacanthis burtoni* (26.9); *Calochaetes coccineus* (46.4); *Cardellina rubrifrons* (9.8); *Cardinalis cardinalis* (42.7); *C. phoeniceus* (41.4); *C. sinuatus* (37.0); *Carduelis ambigua* (14.1); *C. ankoberensis* (14.9); *C. atrata* (16.1); *C. atriceps* (13.5); *C. barbata* (15.5); *C. cannabina* (19.6); *C. carduelis* (16.0); *C. chloris* (26.0); *C. crassirostris* (14.3); *C. cucullata* (9.8); *C. flammea* (13.0); *C. flavirostris* (15.4); *C. hornemanni* (15.5); *C. johannis* (13.4); *C. lawrencei* (10.9); *C. magellanica* (13.6); *C. monguilloti* (19.0); *C. notata* (10.9); *C. olivacea* (10.6); *C. pinus* (12.7); *C. psaltria* (8.8); *C. siemiradzkii* (10.3); *C. sinica* (18.6); *C. spinescens* (11.3); *C. spinoides* (18.6); *C. spinus* (13.3); *C. tristis* (12.8); *C. uropygialis* (14.0); *C. xanthogastra* (12.7); *C. yarrellii* (9.8); *C. yemenensis* (14.3); *Carpodacus cassinii* (26.5); *C. edwardsii* (26.5); *C. eos* (16.0); *C. erythrinus* (24.0); *C. mexicanus* (21.4); *C. nipalensis* (22.3); *C. pulcherrimus* (19.2); *C. puniceus* (46.8); *C. purpureus* (23.3); *C. rhodochlamys* (33.5); *C. rhodochrous* (17.9); *C. roborowskii* (27.4); *C. rodopeplus* (23.0); *C. roseus* (28.6); *C. rubescens* (22.0); *C. rubicilla* (43.2); *C. rubicilloides* (42.1); *C. synoicus* (20.8); *C. thura* (31.4); *C. trifasciatus* (36.0); *C. vinaceus* (22.2); *Caryothraustes canadensis* (34.5); *C. poliogaster* (41.8); *Catamblyrhynchus diadema* (14.2); *Catamenia analis* (12.0); *C. homochroa* (12.2); *C. inornata* (13.4); *Chamaethlypis poliocephala* (15.5); *Charitospiza eucosma* (10.6); *Chlorochrysa calliparaea* (12.5); *C. nitidissima* (18.6); *C. phoenicotis* (22.0); *Chlorophanes spiza* (19.0); *Chlorophonia callophrys* (17.0); *C. cyanea* (14.0); *C. flavirostris* (11.0); *C. occipitalis* (25.8); *C. pyrrhophrys* (17.0); *Chlorornis riefferii* (53.0); *Chlorospingus canigularis* (18.0); *C. flavigularis* (25.6); *C. flavovirens* (25.0); *C. inornatus* (28.0); *C. ophthalmicus* (19.5); *C. parvirostris* (24.0); *C. pileatus* (21.0); *C. semifuscus* (19.0); *C. tacarcunae* (18.9); *Chlorothraupis carmioli* (36.6); *C. frenata* (38.0); *C. olivacea* (39.0); *C. stolzmanni* (38.8); *Chondestes grammacus* (29.0); *Chrysothlypis chrysomelaena* (13.0); *Cissopis leveriana* (76.0); *Clypicterus oseryi* (156.8); *Cnemoscopus rubrirostris* (18.0); *Coccothraustes abeillei* (48.5); *C. coccothraustes* (56.7); *C. vespertinus* (57.6); *Coereba flaveola* (8.3); *Compsospiza baeri* (31.6); *C. garleppi* (31.6); *Compsothraupis loricata* (72.5); *Conirostrum albifrons* (31.5); *C. bicolor* (10.5); *C. cinereum* (8.8); *C. ferrugineiventre* (11.5); *C. leucogenys* (7.0); *C. margaritae* (8.9); *C. rufum* (11.0); *C. sitticolor* (11.9); *C. speciosum* (8.8); *C. tamarugense* (10.5); *Conothraupis speculigera* (25.0); *Coryphaspiza melanotis* (15.7); *Coryphospingus cucullatus* (14.3); *C. pileatus* (15.3); *Creurgops dentata* (19.0); *C. verticalis* (24.0); *Curaeus curaeus* (83.7); *C. forbesi* (64.5); *Cyanerpes caeruleus* (12.0); *C. cyaneus* (14.0); *C. lucidus* (11.4); *C. nitidus* (9.0); *Cyanicterus cyanicterus* (34.0); *Cyanocompsa brissonii* (27.5); *C. cyanoides* (32.5); *C. glaucocaerulea* (18.2); *C. parellina* (15.7); *Cypsnagra hirundinacea* (31.4); *Dacnis albiventris* (11.2); *D. berlepschi* (13.1); *D. cayana* (13.0); *D. egregia* (11.0); *D. flaviventer* (13.0); *D. hartlaubi* (12.1); *D. lineata* (11.0); *D. nigripes* (14.0); *D. venusta* (16.1); *D. viguieri* (11.7); *Delothraupis castaneoventris* (28.0); *Dendroica aestiva* (9.0); *D. caerulescens* (10.2); *D. castanea* (11.8); *D. cerulea* (9.1); *D. chrysoparia* (9.9); *D. coronata* (11.9); *D. discolor* (7.7); *D. dominica* (9.7); *D. fusca* (9.8); *D. graciae* (8.1); *D. kirtlandii* (13.9); *D. magnolia* (8.2); *D. nigrescens* (8.7); *D. occidentalis* (10.0); *D. palmarum* (10.3); *D. pensylvanica* (9.3); *D. petechia* (9.5); *D. pinus* (12.1); *D. striata* (11.9); *D. tigrina* (10.1); *D. townsendi* (8.9); *D. virens* (8.7); *Diglossa albilatera* (9.9); *D. baritula* (9.2); *D. brunneiventris* (12.0); *D. carbonaria* (11.0); *D. duidae* (14.9); *D. gloriosa* (11.0); *D. gloriosissima* (14.0); *D. humeralis* (13.2); *D. lafresnayii* (16.0); *D. major* (22.2); *D. mystacalis* (16.2); *D. plumbea* (10.0); *D. sittoides* (9.0); *D. venezuelensis* (11.8); *Diglossopis caerulescens* (14.5); *D. cyanea* (17.1); *D. glauca* (12.0); *D. indigotica* (13.7); *Diuca diuca* (36.8); *D. speculifera* (34.2); *Dives dives* (91.7); *D. warszewiczi* (73.3); *Dolichonyx oryzivorus* (31.6); *Dolospingus fringilloides* (12.7); *Donacospiza albifrons* (16.0); *Dubusia taeniata* (37.0); *Emberiza affinis* (15.4); *E. aureola* (19.6); *E. bruniceps* (24.9); *E. buchanani* (21.2); *E. cabanisi* (24.9); *E. caesia* (19.9); *E. capensis* (20.9); *E. chrysophrys* (18.0); *E. cia* (23.4); *E. cineracea* (24.3); *E. cioides* (21.1); *E. cirlus* (25.6); *E. citrinella* (29.7); *E. elegans* (16.9); *E. flaviventris* (18.3); *E. fucata* (19.8); *E. godlewskii* (19.0); *E. hortulana* (19.9); *E. impetuani* (15.1); *E. jankowskii* (22.5); *E. koslowi* (16.5); *E. leucocephalos* (28.5); *E. melanocephala* (28.4); *E. pallasi* (14.0); *E. poliopleura* (15.8); *E. pusilla* (14.6); *E. rustica* (20.6); *E. rutila* (17.5); *E. schoeniclus* (18.5); *E. spodocephala* (18.6); *E. stewarti* (16.0); *E. striolata* (14.8); *E. tahapisi* (13.7); *E. tristrami* (18.0); *E. variabilis* (23.8); *E. vincenti* (20.9); *E. yessoensis* (13.5); *Emberizoides duidae* (42.9); *E. herbicola* (27.0); *E. ypiranganus* (20.1); *Embernagra longicauda* (42.9); *E. platensis* (45.5); *Eophona migratoria* (46.9); *E. personata* (80.0); *Ergaticus ruber* (8.1); *E. versicolor* (10.0); *Erythrothlypis salmoni* (17.6); *Eucometis penicillata* (27.0); *Euphagus carolinus* (59.8); *E. cyanocephalus* (62.7); *Euphonia affinis* (10.0); *E. anneae* (14.9); *E. cayennen-*

sis (14.3); *E. chalybea* (19.0); *E. chlorotica* (11.0); *E. chrysopasta* (14.0); *E. concinna* (10.3); *E. cyanocephala* (14.0); *E. elegantissima* (15.0); *E. finschi* (10.5); *E. fulvicrissa* (11.0); *E. gouldi* (14.0); *E. hirundinacea* (14.0); *E. imitans* (14.0); *E. laniirostris* (15.0); *E. luteicapilla* (13.0); *E. mesochrysa* (13.0); *E. minuta* (10.0); *E. pectoralis* (14.4); *E. plumbea* (8.9); *E. rufiventris* (14.0); *E. saturata* (11.8); *E. trinitatis* (11.0); *E. violacea* (15.0); *E. xanthogaster* (13.0); *Euthlypis lachrymosa* (25.6); *Fringilla coelebs* (22.9); *F. montifringilla* (23.2); *Geothlypis aequinoctialis* (13.1); *G. auricularis* (15.0); *G. beldingi* (15.7); *G. chiriquensis* (15.0); *G. flavovelata* (10.9); *G. nelsoni* (11.0); *G. semiflava* (17.2); *G. speciosa* (10.8); *G. trichas* (9.6); *G. velata* (15.0); *Gnorimopsar chopi* (65.9); *Granatellus pelzelni* (11.2); *G. sallaei* (9.9); *G. venustus* (10.8); *Gubernatrix cristata* (47.6); *Gymnomystax mexicanus* (94.0); *Habia atrimaxillaris* (48.9); *H. cristata* (32.9); *H. fuscicauda* (36.9); *H. gutturalis* (33.4); *H. rubica* (32.5); *Haematospiza sipahi* (39.5); *Haplospiza rustica* (15.6); *H. unicolor* (15.3); *Helmitheros vermivorus* (14.2); *Hemispingus atropileus* (22.0); *H. auricularis* (22.0); *H. calophrys* (17.0); *H. frontalis* (17.0); *H. goeringi* (16.5); *H. melanotis* (16.0); *H. ochraceus* (16.0); *H. parodii* (21.8); *H. piurae* (16.0); *H. reyi* (15.7); *H. rufosuperciliaris* (29.0); *H. superciliaris* (14.0); *H. trifasciatus* (14.0); *H. verticalis* (14.0); *H. xanthophthalmus* (12.0); *Hemithraupis flavicollis* (12.8); *H. guira* (12.0); *H. ruficapilla* (11.0); *Heterospingus rubrifrons* (38.0); *H. xanthopygius* (38.8); *Hypopyrrhus pyrohypogaster* (113.5); *Icteria virens* (25.0); *Icterus abeillei* (33.0); *I. auratus* (32.1); *I. auricapillus* (32.2); *I. bullockii* (37.9); *I. cayanensis* (36.0); *I. chrysater* (53.4); *I. chrysocephalus* (41.2); *I. croconotus* (40.7); *I. cucullatus* (24.3); *I. galbula* (32.9); *I. graceannae* (35.8); *I. graduacauda* (42.2); *I. gularis* (55.3); *I. icterus* (57.9); *I. jamacaii* (68.0); *I. maculialatus* (37.4); *I. mesomelas* (29.9); *I. nigrogularis* (40.2); *I. parisorum* (36.5); *I. pectoralis* (46.5); *I. prosthemelas* (28.0); *I. pustulatus* (36.8); *I. spurius* (19.5); *I. wagleri* (41.8); *Idiopsar brachyurus* (43.0); *Incaspiza laeta* (22.0); *I. ortizi* (32.5); *I. personata* (33.3); *I. pulchra* (27.6); *I. watkinsi* (20.4); *Iridophanes pulcherrima* (15.3); *Iridosornis analis* (26.0); *I. jelskii* (20.0); *I. porphyrocephala* (22.9); *I. reinhardti* (24.0); *I. rufivertex* (23.0); *Junco bairdii* (20.0); *J. hyemalis* (19.9); *J. phaeonotus* (20.4); *J. vulcani* (28.0); *Lampropsar tanagrinus* (46.6); *Lamprospiza melanoleuca* (34.0); *Lanio aurantius* (35.0); *L. fulvus* (24.0); *L. leucothorax* (40.0); *L. versicolor* (17.0); *Latoucheornis siemsseni* (23.0); *Leucosticte arctoa* (30.8); *L. atrata* (25.3); *L. australis* (26.6); *L. brandti* (30.4); *L. nemoricola* (22.7); *L. sillemi* (12.3); *L. tephrocotis* (24.6); *Limnothlypis swainsonii* (18.9); *Linurgus olivaceus* (20.3); *Lophospingus griseocristatus* (17.9); *L. pusillus* (14.5); *Loxia curvirostra* (38.3); *L. leucoptera* (29.0); *L. pytyopsittacus* (53.0); *L. scotica* (43.2); *Lysurus castaneiceps* (36.9); *L. crassirostris* (38.8); *Macroagelaius imthurni* (72.7); *M. subalaris* (66.8); *Melanodera melanodera* (28.7); *M. xanthogramma* (35.1); *Melophus lathami* (21.9); *Melospiza georgiana* (16.1); *M. lincolnii* (16.6); *M. melodia* (23.2); *Melozone biarcuatum* (30.6); *M. cabanisi* (36.6); *M. kieneri* (38.7); *M. leucotis* (39.9); *Miliaria calandra* (43.2); *Mitrospingus cassinii* (40.4); *M. oleagineus* (41.3); *Mniotilta varia* (10.9); *Molothrus aeneus* (62.9); *M. armenti* (51.1); *M. ater* (40.7); *M. bonariensis* (50.2); *M. oryzivorus* (184.0); *M. rufoaxillaris* (54.0); *Mycerobas affinis* (76.8); *M. carnipes* (59.1); *M. icterioides* (67.0); *M. melanozanthos* (62.0); *Myioborus albifacies* (10.9); *M. albifrons* (11.0); *M. brunniceps* (9.2); *M. cardonai* (11.2); *M. castaneocapillus* (10.6); *M. flavivertex* (10.8); *M. melanocephalus* (11.3); *M. miniatus* (10.0); *M. ornatus* (11.7); *M. pariae* (10.9); *M. pictus* (7.9); *M. torquatus* (10.5); *Nemosia pileata* (16.0); *N. rourei* (21.6); *Neothraupis fasciata* (26.8); *Nephelornis oneilli* (16.2); *Ocyalus latirostris* (97.5); *Oporornis agilis* (13.3); *O. formosus* (14.0); *O. philadelphia* (11.2); *O. tolmiei* (10.4); *Orchesticus abeillei* (31.5); *Oreomanes fraseri* (25.0); *Oreothraupis arremonops* (39.7); *Oriturus superciliosus* (41.4); *Orthogonys chloricterus* (45.6); *Oryzoborus angolensis* (13.0); *O. atrirostris* (26.0); *O. crassirostris* (20.9); *O. maximiliani* (24.6); *O. nuttingi* (24.0); *Parkerthraustes humeralis* (37.0); *Paroaria baeri* (21.9); *P. capitata* (37.9); *P. coronata* (22.3); *P. dominicana* (33.2); *P. gularis* (23.6); *Parula americana* (8.1); *P. gutturalis* (9.5); *P. pitiayumi* (6.9); *P. superciliosa* (9.0); *Passerculus sandwichensis* (20.6); *Passerella iliaca* (33.3); *Passerina amoena* (15.5); *P. caerulea* (27.4); *P. ciris* (15.6); *P. cyanea* (14.7); *P. leclancherii* (14.0); *P. rositae* (20.0); *P. versicolor* (12.9); *Periporphyrus erythromelas* (48.0); *Pezopetes capitalis* (55.8); *Pheucticus aureoventris* (49.0); *P. chrysogaster* (55.8); *P. chrysopeplus* (77.6); *P. ludovicianus* (42.0); *P. melanocephalus* (47.2); *P. tibialis* (62.3); *Phlogothraupis sanguinolenta* (40.0); *Phrygilus alaudinus* (23.6); *P. atriceps* (24.3); *P. carbonarius* (17.9); *P. dorsalis* (38.2); *P. erythronotus* (26.3); *P. fruticeti* (38.8); *P. gayi* (25.6); *P. patagonicus* (22.6); *P. plebejus* (14.7); *P. punensis* (37.2); *P. unicolor* (21.9); *Piezorhina cinerea* (26.8); *Pinicola enucleator* (56.4); *P. subhimachalus* (46.2); *Pipilo aberti* (46.0); *P. albicollis* (46.5); *P. chlorurus* (46.4); *P. crissalis* (52.9); *P. erythrophthalmus* (40.1); *P. fuscus* (44.4); *P. maculatus* (39.3); *P. ocai* (61.1); *Pipraeidea melanonota* (21.0); *Piranga bidentata* (36.1); *P. erythrocephala* (21.8); *P. flava* (40.0); *P. hepatica* (40.0); *P. leucoptera* (16.0); *P. ludoviciana* (28.1); *P. lutea* (30.0); *P.*

olivacea (28.2); *P. roseogularis* (24.0); *P. rubra* (29.2); *P. rubriceps* (35.9); *Plectrophenax nivalis* (42.2); *Pooecetes gramineus* (25.7); *Poospiza alticola* (22.9); *P. boliviana* (22.9); *P. cinerea* (11.6); *P. erythrophrys* (14.1); *P. hispaniolensis* (16.5); *P. hypochondria* (21.2); *P. lateralis* (19.2); *P. melanoleuca* (13.1); *P. nigrorufa* (17.4); *P. ornata* (11.8); *P. rubecula* (24.8); *P. thoracica* (11.9); *P. torquata* (11.0); *P. whitii* (17.0); *Poospizopsis caesar* (13.9); *Porphyrospiza caerulescens* (13.9); *Protonotaria citrea* (14.3); *Psarocolius angustifrons* (271.0); *P. atrovirens* (152.0); *P. bifasciatus* (277.5); *P. cassini* (262.1); *P. decumanus* (216.0); *P. guatimozinus* (292.9); *P. montezuma* (375.0); *P. viridis* (300.0); *P. yuracares* (360.0); *Pselliophorus luteoviridis* (30.0); *P. tibialis* (30.0); *Pseudochloroptila symonsi* (13.5); *P. totta* (13.5); *Pseudoleistes guirahuro* (86.6); *P. virescens* (80.0); *Pyrrhocoma ruficeps* (15.6); *Pyrrhoplectes epauletta* (19.0); *Pyrrhula aurantiaca* (19.5); *P. erythaca* (19.0); *P. erythrocephala* (22.8); *P. nipalensis* (21.8); *P. pyrrhula* (24.4); *Quiscalus lugubris* (63.7); *Q. major* (159.0); *Q. mexicanus* (169.0); *Q. nicaraguensis* (65.9); *Q. palustris* (138.2); *Q. quiscula* (106.0); *Ramphocelus bresilius* (32.9); *R. carbo* (26.0); *R. costaricensis* (31.0); *R. dimidiatus* (28.0); *R. flammigerus* (33.0); *R. icteronotus* (33.0); *R. melanogaster* (25.0); *R. nigrogularis* (31.0); *R. passerinii* (32.0); *Rhodinocichla rosea* (48.0); *Rhodopechys githagineus* (19.6); *R. mongolica* (21.5); *R. obsoleta* (25.5); *R. sanguinea* (38.2); *Rhodospingus cruentus* (11.6); *Rhodothraupis celaeno* (60.0); *Rhynchostruthus socotranus* (31.5); *Saltator atriceps* (83.9); *S. atripennis* (55.0); *S. aurantiirostris* (42.0); *S. cinctus* (48.6); *S. coerulescens* (54.9); *S. fuliginosus* (59.9); *S. grossus* (44.2); *S. maxillosus* (50.8); *S. maximus* (47.7); *S. nigriceps* (59.9); *S. orenocensis* (33.7); *S. rufiventris* (59.9); *S. similis* (43.3); *S. striatipectus* (39.0); *Saltatricula multicolor* (22.2); *Schistochlamys melanopis* (33.0); *S. ruficapillus* (31.2); *Seiurus aurocapillus* (18.8); *S. motacilla* (19.9); *S. noveboracensis* (16.3); *Sericossypha albocristata* (114.0); *Serinus albogularis* (27.1); *S. atrogularis* (11.4); *S. buchanani* (19.1); *S. burtoni* (30.5); *S. canaria* (24.3); *S. canicollis* (15.2); *S. capistratus* (14.6); *S. citrinella* (12.0); *S. citrinelloides* (13.0); *S. citrinipectus* (11.2); *S. donaldsoni* (24.0); *S. dorsostriatus* (15.2); *S. flavigula* (18.7); *S. flaviventris* (16.2); *S. flavivertex* (14.0); *S. frontalis* (12.3); *S. gularis* (16.0); *S. hypostictus* (13.0); *S. koliensis* (13.6); *S. leucopterus* (22.1); *S. leucopygius* (10.8); *S. melanochrous* (14.6); *S. menachensis* (19.2); *S. mennelli* (15.4); *S. mozambicus* (11.9); *S. nigriceps* (14.6); *S. pusillus* (11.6); *S. reichardi* (15.5); *S. reichenowi* (10.9); *S. rothschildi* (14.0); *S. scotops* (14.2); *S. serinus* (11.2); *S. striolatus* (22.4); *S. sulphuratus* (27.9); *S. syriacus* (11.7); *S. thibetanus* (10.5); *S. tristriatus* (15.5); *S. whytii* (16.7); *S. xantholaemus* (11.8); *S. xanthopygius* (12.0); *Setophaga ruticilla* (8.3); *Sicalis auriventris* (55.0); *S. citrina* (11.6); *S. columbiana* (13.4); *S. flaveola* (17.0); *S. lebruni* (25.3); *S. lutea* (13.0); *S. luteocephala* (19.8); *S. luteola* (15.9); *S. olivascens* (21.8); *S. raimondii* (15.8); *S. taczanowskii* (12.5); *S. uropygialis* (22.5); *Spiza americana* (26.3); *Spizella arborea* (17.9); *S. atrogularis* (11.3); *S. breweri* (10.9); *S. pallida* (11.2); *S. passerina* (12.2); *S. pusilla* (12.5); *S. wortheni* (12.4); *Sporophila albogularis* (9.7); *S. americana* (12.0); *S. bouvreuil* (8.6); *S. bouvronides* (9.1); *S. caerulescens* (9.8); *S. castaneiventris* (7.8); *S. cinnamomea* (10.9); *S. collaris* (13.5); *S. corvina* (10.7); *S. falcirostris* (11.0); *S. frontalis* (14.3); *S. hypochroma* (9.7); *S. hypoxantha* (9.5); *S. insulata* (9.5); *S. intermedia* (12.1); *S. leucoptera* (15.5); *S. lineola* (9.8); *S. luctuosa* (12.5); *S. melanogaster* (9.3); *S. melanops* (11.0); *S. minuta* (7.8); *S. murallae* (11.0); *S. nigricollis* (9.6); *S. nigrorufa* (10.9); *S. palustris* (8.3); *S. peruviana* (12.6); *S. plumbea* (9.7); *S. ruficollis* (8.6); *S. schistacea* (12.7); *S. simplex* (11.0); *S. telasco* (9.6); *S. torqueola* (9.0); *S. zelichi* (10.9); *Stephanophorus diadematus* (35.4); *Sturnella bellicosa* (58.0); *S. defilippi* (67.5); *S. loyca* (113.0); *S. magna* (93.0); *S. militaris* (40.9); *S. neglecta* (101.0); *S. superciliaris* (45.8); *Tachyphonus coronatus* (29.3); *T. cristatus* (18.8); *T. delatrii* (18.0); *T. luctuosus* (13.0); *T. phoenicius* (21.0); *T. rufiventer* (19.0); *T. rufus* (34.4); *T. surinamus* (19.0); *Tangara argyrofenges* (19.0); *T. arthus* (22.0); *T. brasiliensis* (20.0); *T. cabanisi* (25.5); *T. callophrys* (22.9); *T. cayana* (18.0); *T. chilensis* (20.0); *T. chrysotis* (24.0); *T. cyanicollis* (17.0); *T. cyanocephala* (18.0); *T. cyanoptera* (21.6); *T. cyanotis* (15.0); *T. cyanoventris* (16.5); *T. desmaresti* (20.4); *T. dowii* (20.0); *T. fastuosa* (20.8); *T. florida* (19.3); *T. fucosa* (21.0); *T. guttata* (18.4); *T. gyrola* (22.0); *T. heinei* (20.2); *T. icterocephala* (22.0); *T. inornata* (18.0); *T. johannae* (20.8); *T. labradorides* (15.0); *T. larvata* (20.0); *T. lavinia* (24.0); *T. mexicana* (20.5); *T. meyerdeschauenseei* (26.0); *T. nigrocincta* (17.0); *T. nigroviridis* (17.0); *T. palmeri* (32.3); *T. parzudakii* (28.0); *T. peruviana* (22.2); *T. phillipsi* (19.9); *T. preciosa* (22.8); *T. punctata* (15.0); *T. ruficervix* (19.0); *T. rufigenis* (16.5); *T. rufigula* (19.1); *T. schrankii* (19.0); *T. seledon* (18.7); *T. varia* (10.0); *T. vassorii* (18.0); *T. velia* (21.0); *T. viridicollis* (21.0); *T. vitriolina* (23.0); *T. xanthocephala* (19.0); *T. xanthogastra* (15.0); *Tersina viridis* (29.0); *Thlypopsis fulviceps* (12.0); *T. inornata* (15.0); *T. ornata* (12.0); *T. pectoralis* (15.0); *T. ruficeps* (11.0); *T. sordida* (17.0); *Thraupis abbas* (45.0); *T. bonariensis* (36.0); *T. cyanocephala* (36.0); *T. cyanoptera* (43.3); *T. episcopus* (35.0); *T. glaucocolpa* (31.6); *T. ornata* (33.0); *T. palmarum* (39.0); *T. sayaca* (32.5); *Tiaris bicolor* (9.8);

T. fuliginosa (13.3); *T. obscura* (11.2); *T. olivacea* (9.8); *Trichothraupis melanops* (24.3); *Uragus sibiricus* (17.5); *Urocynchramus pylzowi* (25.0); *Urothraupis stolzmanni* (23.1); *Vermivora bachmanii* (9.2); *V. celata* (9.2); *V. chrysoptera* (8.8); *V. crissalis* (9.3); *V. luciae* (6.6); *V. peregrina* (8.9); *V. pinus* (8.9); *V. ruficapilla* (8.1); *V. virginiae* (8.2); *Volatinia jacarina* (10.0); *Wetmorethraupis sterrhopteron* (50.2); *Wilsonia canadensis* (10.1); *W. citrina* (10.6); *W. pusilla* (6.6); *Xanthocephalus xanthocephalus* (64.5); *Xanthopsar flavus* (22.1); *Xenodacnis parina* (11.5); *Xenospingus concolor* (21.0); *Xenospiza baileyi* (17.4); *Zarhynchus wagleri* (175.0); *Zeledonia coronata* (21.0); *Zonotrichia albicollis* (24.4); *Z. atricapilla* (32.0); *Z. capensis* (20.3); *Z. leucophrys* (28.1); *Z. querula* (33.7); *Acrobatornis fonsecai* (13.7); *Anabacerthia striaticollis* (24.8); *A. variegaticeps* (27.8); *Anabazenops dorsalis* (35.4); *A. fuscus* (39.0); *Ancistrops strigilatus* (35.9); *Anumbius annumbi* (41.5); *Aphrastura spinicauda* (11.5); *Asthenes anthoides* (22.3); *A. arequipae* (20.3); *A. baeri* (17.8); *A. berlepschi* (24.4); *A. cactorum* (17.5); *A. dorbignyi* (15.9); *A. flammulata* (22.5); *A. heterura* (13.5); *A. huancavelicae* (20.3); *A. hudsoni* (30.8); *A. humicola* (22.5); *A. humilis* (15.2); *A. luizae* (28.0); *A. maculicauda* (19.0); *A. modesta* (16.8); *A. ottonis* (13.0); *A. patagonica* (16.4); *A. pudibunda* (15.0); *A. pyrrholeuca* (13.2); *A. sclateri* (25.9); *A. steinbachi* (19.5); *A. urubambensis* (16.0); *A. virgata* (22.0); *A. wyatti* (15.2); *Automolus infuscatus* (32.9); *A. leucophthalmus* (34.5); *A. melanopezus* (39.8); *A. ochrolaemus* (40.2); *A. roraimae* (27.6); *A. rubiginosus* (39.8); *A. rufipileatus* (34.8); *Berlepschia rikeri* (37.0); *Campylorhamphus falcularius* (42.6); *C. procurvoides* (33.5); *C. pucherani* (20.3); *C. pusillus* (40.5); *C. trochilirostris* (70.5); *Certhiaxis cinnamomea* (15.2); *C. mustelina* (15.0); *Chilia melanura* (40.0); *Cichlocolaptes leucophrus* (40.8); *Cinclodes antarcticus* (63.2); *C. aricomae* (50.0); *C. atacamensis* (53.0); *C. comechingonus* (28.5); *C. excelsior* (64.0); *C. fuscus* (30.0); *C. nigrofumosus* (65.0); *C. oustaleti* (30.5); *C. pabsti* (53.0); *C. palliatus* (104.0); *C. patagonicus* (30.7); *C. taczanowskii* (64.5); *Clibanornis dendrocolaptoides* (48.2); *Coryphistera alaudina* (30.0); *Cranioleuca albicapilla* (21.5); *C. albiceps* (17.8); *C. antisiensis* (17.0); *C. baroni* (21.8); *C. curtata* (17.5); *C. demissa* (15.2); *C. erythrops* (16.9); *C. gutturata* (14.9); *C. hellmayri* (15.0); *C. henricae* (14.9); *C. marcapatae* (19.8); *C. muelleri* (14.5); *C. obsoleta* (13.4); *C. pallida* (11.5); *C. pyrrhophia* (14.9); *C. semicinerea* (15.0); *C. subcristata* (14.7); *C. sulphurifera* (13.5); *C. vulpecula* (19.0); *C. vulpina* (15.7); *Deconychura longicauda* (23.8); *D. stictolaema* (18.5); *Dendrexetastes rufigula* (69.6); *Dendrocincla anabatina* (34.4); *D. fuliginosa* (38.7); *D. homochroa* (38.9); *D. merula* (53.3); *D. turdina* (39.0); *D. tyrannina* (54.9); *Dendrocolaptes certhia* (68.7); *D. hoffmannsi* (83.0); *D. picumnus* (67.4); *D. platyrostris* (61.7); *D. sanctithomae* (66.9); *Drymornis bridgesii* (94.0); *Eremobius phoenicurus* (30.2); *Furnarius cinnamomeus* (14.0); *F. cristatus* (25.5); *F. figulus* (28.0); *F. leucopus* (54.8); *F. longirostris* (44.0); *F. minor* (26.0); *F. rufus* (70.5); *F. torridus* (52.5); *Geobates poecilopterus* (9.5); *Geositta antarctica* (37.0); *G. crassirostris* (55.8); *G. cunicularia* (28.5); *G. isabellina* (43.0); *G. maritima* (16.5); *G. peruviana* (20.8); *G. punensis* (25.8); *G. rufipennis* (26.6); *G. saxicolina* (33.0); *G. tenuirostris* (32.5); *Glyphorynchus spirurus* (14.6); *Gyalophylax hellmayri* (24.5); *Heliobletus contaminatus* (14.0); *Hellmayrea gularis* (12.4); *Hylexetastes brigidai* (115.0); *H. perrotii* (104.0); *H. stresemanni* (111.0); *H. uniformis* (93.2); *Hylocryptus erythrocephalus* (46.5); *H. rectirostris* (48.0); *Hyloctistes subulatus* (28.8); *H. virgatus* (33.0); *Lepidocolaptes affinis* (35.0); *L. albolineatus* (20.3); *L. angustirostris* (29.7); *L. falcinellus* (28.0); *L. fuscus* (21.8); *L. lacrymiger* (30.6); *L. leucogaster* (36.0); *L. souleyetii* (25.7); *L. squamatus* (28.1); *L. wagleri* (27.0); *Leptasthenura aegithaloides* (10.9); *L. andicola* (15.5); *L. fuliginiceps* (12.6); *L. pileata* (10.3); *L. platensis* (10.6); *L. setaria* (11.0); *L. striata* (9.0); *L. striolata* (10.5); *L. xenothorax* (10.5); *L. yanacensis* (8.8); *Limnoctites rectirostris* (22.6); *Limnornis curvirostris* (28.6); *Lochmias nematura* (22.0); *Margarornis bellulus* (18.5); *M. rubiginosus* (17.8); *M. squamiger* (17.3); *M. stellatus* (21.5); *Megaxenops parnaguae* (25.0); *Metopothrix aurantiacus* (11.2); *Nasica longirostris* (92.0); *Oreophylax moreirae* (10.5); *Phacellodomus dorsalis* (36.0); *P. erythrophthalmus* (24.5); *P. inornatus* (72.3); *P. maculipectus* (21.9); *P. ruber* (41.0); *P. rufifrons* (24.6); *P. sibilatrix* (15.5); *P. striaticeps* (29.1); *P. striaticollis* (25.7); *Philydor amaurotis* (18.8); *P. atricapillus* (22.2); *P. dimidiatus* (29.4); *P. erythrocercus* (26.4); *P. erythropterus* (30.0); *P. fuscipennis* (26.5); *P. lichtensteini* (21.0); *P. novaesi* (38.0); *P. pyrrhodes* (30.5); *P. ruficaudatus* (30.1); *P. rufus* (25.0); *Phleocryptes melanops* (14.6); *Premnoplex brunnescens* (16.3); *P. tatei* (16.1); *Premnornis guttuligera* (16.0); *Pseudocolaptes boissonneautii* (43.9); *P. johnsoni* (39.7); *P. lawrencii* (51.0); *Pseudoseisura cristata* (47.6); *P. gutturalis* (70.4); *P. lophotes* (76.0); *P. unirufa* (44.9); *Pygarrhichas albogularis* (24.0); *Roraimia adusta* (16.3); *Schizoeaca coryi* (16.8); *S. fuliginosa* (18.3); *S. griseomurina* (17.6); *S. harterti* (12.9); *S. helleri* (15.3); *S. palpebralis* (17.0); *S. perijana* (18.5); *S. vilcabambae* (20.2); *Schoeniophylax phryganophila* (18.6); *Sclerurus albigularis* (34.8); *S. caudacutus* (35.3); *S. guatemalensis* (34.7); *S. mexicanus* (25.1); *S. rufigularis* (21.6); *S. scansor* (36.9); *Simoxenops striatus* (41.6); *S. ucaya-*

lae (49.8); *Siptornis striaticollis* (41.6); *Siptornopsis hypochondriacus* (24.5); *Sittasomus griseicapillus* (14.2); *Spartonoica maluroides* (11.0); *Sylviorthorhynchus desmursii* (10.9); *Synallaxis albescens* (11.2); *S. albigularis* (15.4); *S. albilora* (15.0); *S. azarae* (16.9); *S. brachyura* (18.3); *S. cabanisi* (22.7); *S. candei* (15.0); *S. castanea* (15.0); *S. cherriei* (16.0); *S. chinchipensis* (15.3); *S. cinerascens* (13.1); *S. cinnamomea* (18.4); *S. courseni* (16.8); *S. erythrothorax* (17.1); *S. frontalis* (14.0); *S. fuscorufa* (16.0); *S. gujanensis* (18.1); *S. hypospodia* (16.4); *S. infuscata* (18.2); *S. kollari* (16.4); *S. macconnelli* (19.5); *S. maranonica* (13.0); *S. moesta* (22.5); *S. propinqua* (20.0); *S. ruficapilla* (13.8); *S. rutilans* (16.7); *S. scutata* (12.3); *S. simoni* (16.6); *S. spixi* (12.6); *S. stictothorax* (10.2); *S. subpudica* (18.2); *S. tithys* (15.8); *S. unirufa* (17.9); *S. whitneyi* (16.2); *S. zimmeri* (13.0); *Syndactyla guttulata* (36.0); *S. ruficollis* (31.0); *S. rufosuperciliata* (25.6); *S. subalaris* (28.9); *Thripadectes flammulatus* (55.9); *T. holostictus* (40.7); *T. ignobilis* (47.2); *T. melanorhynchus* (44.3); *T. rufobrunneus* (56.2); *T. scrutator* (66.3); *T. virgaticeps* (65.8); *Thripophaga berlepschi* (28.3); *T. cherriei* (19.9); *T. fusciceps* (29.4); *T. macroura* (30.2); *Upucerthia albigula* (39.9); *U. andaecola* (31.0); *U. certhioides* (32.8); *U. dumetaria* (48.7); *U. harterti* (32.2); *U. jelskii* (40.1); *U. ruficauda* (36.3); *U. serrana* (48.7); *U. validirostris* (33.6); *Xenerpestes minlosi* (11.0); *X. singularis* (11.6); *Xenops milleri* (12.2); *X. minutus* (10.6); *X. rutilans* (12.2); *X. tenuirostris* (9.7); *Xiphocolaptes albicollis* (118.0); *X. falcirostris* (110.0); *X. major* (156.0); *X. promeropirhynchus* (95.5); *Xiphorhynchus erythropygius* (46.8); *X. eytoni* (58.8); *X. flavigaster* (47.9); *X. guttatus* (58.8); *X. lachrymosus* (56.4); *X. necopinus* (35.8); *X. obsoletus* (32.6); *X. ocellatus* (37.0); *X. pardalotus* (34.7); *X. picus* (40.2); *X. spixii* (31.2); *X. susurrans* (45.8); *X. triangularis* (46.3); *Brachygalba albogularis* (13.6); *B. goeringi* (16.0); *B. lugubris* (15.9); *B. salmoni* (17.3); *Galbalcyrhynchus leucotis* (47.0); *G. purusianus* (50.0); *Galbula albirostris* (22.1); *G. chalcothorax* (24.0); *G. cyanescens* (25.3); *G. cyanicollis* (23.5); *G. dea* (27.4); *G. galbula* (23.0); *G. leucogastra* (15.9); *G. pastazae* (31.8); *G. ruficauda* (26.5); *G. tombacea* (23.3); *Jacamaralcyon tridactyla* (18.4); *Jacamerops aureus* (62.9); *Gavia adamsii* (5057.0); *G. arctica* (3080.0); *G. immer* (4980.0); *G. pacifica* (1669.0); *G. stellata* (1486.0); *Cursorius africanus* (91.8); *C. chalopterus* (155.5); *C. cinctus* (125.0); *C. coromandelicus* (145.0); *C. cursor* (138.0); *C. rufus* (75.0); *C. temminckii* (69.2); *Dromas ardeola* (325.0); *Glareola cinerea* (37.4); *G. lactea* (39.8); *G. maldivarum* (75.2); *G. nordmanni* (97.2); *G. nuchalis* (62.7); *G. ocularis* (92.5); *G. pratincola* (84.9); *Pluvianus aegyptius* (82.0); *Rhinoptilus bitorquatus* (170.0); *Stiltia isabella* (65.5); *Anthropoides paradisea* (2400.0); *A. virgo* (2417.0); *Balearica pavonia* (3590.0); *B. regulorum* (3772.0); *Bugeranus carunculatus* (8159.0); *Grus americana* (5826.0); *G. antigone* (5959.0); *G. canadensis* (4391.0); *G. grus* (5500.0); *G. japonensis* (8786.0); *G. leucogeranus* (5931.0); *G. monacha* (3735.0); *G. nigricollis* (6000.0); *G. rubicunda* (6251.0); *G. vipio* (4663.0); *Heliopais personata* (1080.0); *Heliornis fulica* (132.0); *Podica senegalensis* (599.0); *Aramus guarauna* (1080.0); *Hemiprocne comata* (20.8); *H. coronata* (29.0); *H. longipennis* (42.8); *Alopochelidon fucata* (14.0); *Atticora fasciata* (13.0); *A. melanoleuca* (10.8); *Cheramoeca leucosternus* (14.1); *Delichon dasypus* (18.0); *D. nipalensis* (15.0); *D. urbica* (14.5); *Haplochelidon andecola* (13.1); *Hirundo abyssinica* (13.5); *H. aethiopica* (13.3); *H. albigularis* (21.8); *H. angolensis* (17.8); *H. ariel* (10.9); *H. atrocaerulea* (13.8); *H. concolor* (13.0); *H. cucullata* (27.1); *H. daurica* (22.2); *H. dimidiata* (12.1); *H. fluvicola* (9.7); *H. fuliginosa* (10.0); *H. fuligula* (21.1); *H. leucosoma* (14.0); *H. lucida* (13.0); *H. megaensis* (11.0); *H. neoxena* (14.7); *H. nigricans* (15.4); *H. nigrita* (18.9); *H. nigrorufa* (14.2); *H. preussi* (13.3); *H. rufigula* (15.9); *H. rupestris* (20.4); *H. rustica* (18.5); *H. semirufa* (30.1); *H. senegalensis* (45.4); *H. smithii* (12.4); *H. spilodera* (20.6); *H. striolata* (22.0); *H. tahitica* (17.8); *Neochelidon tibialis* (10.6); *Notiochelidon cyanoleuca* (10.3); *N. pileata* (12.2); *Petrochelidon fulva* (21.0); *P. pallida* (24.3); *P. pyrrhonota* (21.6); *P. rufocollaris* (16.0); *Phedina brazzae* (13.0); *Progne chalybea* (41.4); *P. elegans* (50.6); *P. murphyi* (44.9); *P. sinaloae* (42.6); *P. subis* (53.8); *P. tapera* (32.0); *Psalidoprocne albiceps* (11.2); *P. nitens* (9.8); *P. obscura* (9.4); *P. pristoptera* (10.4); *Pseudhirundo griseopyga* (8.2); *Pseudochelidon eurystomina* (14.0); *Pygochelidon flavipes* (9.4); *P. murina* (12.5); *Riparia cincta* (23.5); *R. congica* (12.0); *R. diluta* (13.0); *R. paludicola* (13.5); *R. riparia* (12.8); *Stelgidopteryx ridgwayi* (16.0); *S. ruficollis* (16.1); *S. serripennis* (15.7); *Tachycineta albilinea* (16.7); *T. albiventer* (16.7); *T. bicolor* (21.2); *T. meyeni* (14.9); *T. stolzmanni* (11.3); *Hypocolius ampelinus* (53.3); *Indicator archipelagicus* (32.4); *I. conirostris* (31.5); *I. exilis* (17.9); *I. indicator* (50.4); *I. maculatus* (46.8); *I. meliphilus* (14.2); *I. minor* (28.2); *I. pumilio* (13.2); *I. variegatus* (48.8); *I. willcocksi* (15.4); *I. xanthonotus* (30.5); *Melichneutes robustus* (54.2); *Melignomon eisentrauti* (24.2); *M. zenkeri* (23.6); *Prodotiscus insignis* (10.4); *P. regulus* (14.1); *P. zambesiae* (10.2); *Chloropsis aurifrons* (32.5); *C. cochinchinensis* (24.5); *C. cyanopogon* (22.0); *C. hardwickii* (32.8); *C. sonnerati* (33.9); *Irena puella* (64.9); *Actophilornis africana* (199.0); *Hydrophasianus chirurgus* (164.0); *Irediparra gallinacea* (103.0); *Jacana jacana* (108.0); *J. spinosa* (95.5); *Metopidius indicus* (155.0); *Microparra capensis*

(41.3); *Corvinella corvina* (65.4); *Eurocephalus anguitimens* (69.1); *E. rueppelli* (50.7); *Lanius bucephalus* (39.8); *L. cabanisi* (73.9); *L. collaris* (36.7); *L. collurio* (28.5); *L. collurioides* (26.0); *L. cristatus* (48.3); *L. dorsalis* (49.9); *L. excubitor* (63.5); *L. excubitoroides* (53.8); *L. gubernator* (23.5); *L. isabellinus* (25.2); *L. ludovicianus* (51.8); *L. mackinnoni* (34.3); *L. meridionalis* (50.0); *L. minor* (46.5); *L. nubicus* (20.4); *L. schach* (51.6); *L. senator* (36.0); *L. somalicus* (45.3); *L. sphenocercus* (92.1); *L. tephronotus* (46.8); *L. tigrinus* (30.2); *L. vittatus* (20.8); *Urolestes melanoleucus* (70.0); *Chlidonias hybrida* (83.9); *C. leucopterus* (54.2); *C. niger* (65.3); *Larus argentatus* (1094.0); *L. brunnicephalus* (573.0); *L. cachinnans* (1117.0); *L. californicus* (776.0); *L. canus* (427.0); *L. cirrocephalus* (381.0); *L. delawarensis* (519.0); *L. dominicanus* (965.0); *L. fascus* (766.0); *L. genei* (281.0); *L. hyperboreus* (1544.0); *L. ichthyaetus* (1394.0); *L. maculipennis* (339.0); *L. melanocihalus* (256.0); *L. minutus* (118.0); *L. novaehollandiae* (289.0); *L. philadelphia* (211.0); *L. pipixcan* (280.0); *L. ridibundus* (284.0); *L. saundersi* (198.0); *L. serranus* (478.0); *L. thayeri* (946.0); *Lopholaimus antarcticus* (497.0); *Phaetusa simplex* (235.0); *Phaps chalcoptera* (331.0); *P. elegans* (212.0); *P. histrionica* (289.0); *Rhodostethia rosea* (187.0); *Rynchops albicollis* (233.0); *R. flavirostris* (164.0); *R. niger* (302.0); *Stercorarius longicaudus* (289.0); *S. parasiticus* (446.0); *S. pomarinus* (694.0); *Sterna acuticauda* (178.0); *S. albifrons* (48.8); *S. aleutica* (120.0); *S. aurantia* (271.0); *S. caspia* (661.0); *S. forsteri* (149.0); *S. hirundo* (229.5); *S. nereis* (72.3); *S. nilotica* (170.0); *S. paradisaea* (110.0); *S. sandvicensis* (208.0); *S. superciliaris* (46.0); *S. trudeaui* (153.0); *Xema sabini* (198.0); *Buccanodon duchaillui* (41.8); *Gymnobucco bonapartei* (63.0); *G. calvus* (54.6); *G. peli* (53.0); *G. sladeni* (56.9); *Lybius bidentatus* (79.5); *L. chaplini* (69.5); *L. dubius* (91.0); *L. guifsobalito* (42.2); *L. leucocephalus* (62.8); *L. melanopterus* (52.4); *L. minor* (46.7); *L. rolleti* (101.0); *L. rubrifacies* (44.0); *L. torquatus* (51.7); *L. undatus* (38.5); *L. vieilloti* (36.0); *Pogoniulus atroflavus* (18.2); *P. bilineatus* (13.2); *P. chrysoconus* (10.8); *P. coryphaeus* (10.7); *P. leucomystax* (11.8); *P. makawai* (10.0); *P. pusillus* (9.6); *P. scolopaceus* (14.5); *P. simplex* (8.8); *P. subsulphureus* (10.5); *Stactolaema anchietae* (47.3); *S. leucotis* (54.9); *S. olivacea* (49.4); *S. whytii* (55.6); *Trachyphonus darnaudii* (36.7); *T. erythrocephalus* (63.5); *T. margaritatus* (55.0); *T. purpuratus* (76.1); *T. vaillantii* (69.5); *Tricholaema diademata* (30.6); *T. frontata* (27.0); *T. hirsuta* (55.2); *T. lachrymosa* (22.9); *T. leucomelaina* (32.2); *T. melanocephala* (20.5); *Amytornis barbatus* (18.4); *A. dorotheae* (23.3); *A. goyderi* (16.7); *A. housei* (29.0); *A. purnelli* (21.0); *A. striatus* (19.7); *A. textilis* (23.1); *A. woodwardi* (35.1); *Malurus amabilis* (8.7); *M. coronatus* (11.1); *M. cyaneus* (10.1); *M. elegans* (9.6); *M. lamberti* (8.0); *M. leucopterus* (7.4); *M. melanocephalus* (7.9); *M. pulcherrimus* (9.2); *M. splendens* (9.4); *Stipiturus malachurus* (7.3); *S. mallee* (5.5); *S. ruficeps* (5.0); *Calorhamphus fuliginosus* (42.6); *Megalaima asiatica* (90.5); *M. australis* (33.3); *M. chrysopogon* (151.0); *M. faiostricta* (85.0); *M. franklinii* (63.5); *M. haemacephala* (44.6); *M. henricii* (74.1); *M. incognita* (77.0); *M. lagrandieri* (150.0); *M. lineata* (148.0); *M. mystacophanos* (77.4); *M. oorti* (87.7); *M. rafflesii* (118.0); *M. rubricapilla* (37.6); *M. virens* (202.0); *M. viridis* (80.5); *M. zeylanica* (119.0); *Psilopogon pyrolophus* (129.0); *Alectura lathami* (2340.0); *Leipoa ocellata* (1918.0); *Megapodius reinwardt* (993.0); *Acanthagenys rufogularis* (47.8); *Acanthorhynchus superciliosus* (9.8); *A. tenuirostris* (11.2); *Anthocaera carunculata* (106.4); *A. chrysoptera* (68.4); *Ashbyia lovensis* (17.5); *Certhionyx niger* (9.9); *C. pectoralis* (10.1); *C. variegatus* (26.3); *Conopophila albogularis* (11.8); *C. rufogularis* (10.8); *C. whitei* (9.8); *Entomyzon cyanotis* (105.6); *Ephthianura crocea* (9.3); *Epthianura albifrons* (13.3); *E. aurifrons* (10.5); *E. tricolor* (10.7); *Glycichaera fallax* (11.2); *Grantiella picta* (21.5); *Lichenostomus chrysops* (17.3); *L. cratitius* (20.4); *L. fasciogularis* (26.9); *L. flavescens* (12.5); *L. flavicollis* (29.0); *L. flavus* (21.4); *L. frenatus* (34.2); *L. fuscus* (17.9); *L. hindwoodi* (23.0); *L. keartlandi* (15.3); *L. leucotis* (24.0); *L. melanops* (32.4); *L. ornatus* (17.7); *L. penicillatus* (19.4); *L. plumulus* (16.5); *L. unicolor* (30.8); *L. versicolor* (42.3); *L. virescens* (23.4); *Lichmera indistincta* (13.4); *Manorina flavigula* (56.3); *M. melanocephala* (60.3); *M. melanophrys* (30.5); *M. melanotis* (54.0); *Meliphaga albilineata* (23.8); *M. gracilis* (15.0); *M. lewinii* (33.7); *M. notata* (26.5); *Melithreptus albogularis* (11.1); *M. brevirostris* (12.6); *M. gularis* (19.5); *M. lunatus* (14.1); *Myzomela erythrocephala* (8.0); *M. obscura* (12.0); *M. sanguinolenta* (8.4); *Philemon argenticeps* (80.5); *P. buceroides* (95.9); *P. citreogularis* (60.6); *P. corniculatus* (154.5); *Phylidonyris albifrons* (17.5); *P. melanops* (18.3); *P. nigra* (18.3); *P. novaehollandiae* (20.3); *P. pyrrhoptera* (12.8); *Plectorhyncha lanceolata* (34.0); *Ramsayornis fasciatus* (12.1); *R. modestus* (12.8); *Trichodere cockerelli* (16.9); *Xanthomyza phrygia* (40.2); *Xanthotis flaviventer* (35.7); *X. macleayana* (31.2); *Atrichornis clamosus* (43.1); *A. rufescens* (24.0); *Menura alberti* (928.0); *M. novaehollandiae* (980.0); *Merops albicollis* (25.9); *M. apiaster* (56.6); *M. boehmi* (16.6); *M. breweri* (50.0); *M. bullocki* (23.1); *M. bullockoides* (34.8); *M. gularis* (27.3); *M. hirundineus* (21.7); *M. leschenaulti* (27.2); *M. malimbicus* (50.5); *M. muelleri* (22.5); *M. nubicus* (42.4); *M. oreobates* (24.1); *M. orientalis* (14.8); *M. ornatus* (29.5); *M. persicus* (49.3);

M. philippinus (34.0); *M. pusillus* (15.1); *M. revoilii* (13.0); *M. superciliosus* (38.5); *M. variegatus* (22.5); *M. viridis* (34.8); *Nyctyornis athertoni* (84.8); *Aspatha gularis* (62.7); *Baryphthengus martii* (166.0); *B. ruficapillus* (143.0); *Electron carinatum* (64.9); *E. platyrhynchum* (73.0); *Eumomota superciliosa* (62.5); *Hylomanes momotula* (29.3); *Momotus aequatorialis* (158.0); *M. mexicanus* (75.7); *M. momota* (120.0); *Alethe choloensis* (41.3); *A. diademata* (31.2); *A. fuelleborni* (52.0); *A. poliocephala* (32.7); *A. poliophrys* (35.2); *Arcanator orostruthus* (32.7); *Brachypteryx hyperythra* (19.4); *B. leucophrys* (15.8); *B. major* (17.7); *B. montana* (17.7); *B. stellata* (23.0); *Catharus aurantiirostris* (29.8); *C. bicknelli* (27.8); *C. dryas* (37.7); *C. frantzii* (28.9); *C. fuscater* (33.7); *C. fuscescens* (31.9); *C. gracilirostris* (21.0); *C. guttatus* (30.1); *C. mexicanus* (33.0); *C. minimus* (31.6); *C. occidentalis* (26.2); *C. ustulatus* (30.3); *Cercomela dubia* (21.0); *C. familiaris* (19.6); *C. fusca* (12.7); *C. melanura* (15.2); *C. schlegelii* (23.3); *C. scotocerca* (16.0); *C. sinuata* (18.1); *C. sordida* (21.0); *C. tractrac* (20.8); *Cercotrichas barbata* (21.0); *C. coryphaeus* (20.4); *C. galactotes* (20.3); *C. hartlaubi* (19.2); *C. leucophrys* (16.5); *C. leucosticta* (25.5); *C. paena* (19.7); *C. podobe* (24.0); *C. quadrivirgata* (26.1); *C. signata* (38.2); *Chaimarrornis leucocephalus* (30.4); *Cichladusa arquata* (34.2); *C. guttata* (23.2); *C. ruficauda* (29.5); *Cinclidium frontale* (25.4); *C. leucurum* (27.0); *Cochoa purpurea* (103.0); *C. viridis* (107.0); *Copsychus malabaricus* (29.4); *C. saularis* (36.0); *Cossypha albicapilla* (58.5); *C. anomala* (24.5); *C. archeri* (13.0); *C. caffra* (28.5); *C. cyanocampter* (26.7); *C. dichroa* (23.0); *C. heinrichi* (60.5); *C. heuglini* (34.9); *C. humeralis* (22.8); *C. isabellae* (24.0); *C. natalensis* (34.1); *C. niveicapilla* (36.7); *C. polioptera* (18.9); *C. semirufa* (27.3); *Cossyphicula roberti* (16.0); *Cyanoptila cyanomelana* (22.5); *Cyornis banyumas* (14.5); *C. concretus* (22.0); *C. hainanus* (19.0); *C. pallipes* (19.0); *C. poliogenys* (21.0); *C. rubeculoides* (14.2); *C. tickelliae* (16.3); *C. turcosus* (14.0); *C. unicolor* (21.0); *Empidornis semipartitus* (22.5); *Enicurus immaculatus* (25.5); *E. leschenaulti* (33.8); *E. maculatus* (41.0); *E. ruficapillus* (28.3); *E. schistaceus* (31.0); *E. scouleri* (15.9); *Erithacus rubecula* (16.8); *Eumyias albicaudata* (16.4); *E. thalassina* (18.1); *Ficedula albicollis* (12.7); *F. dumetoria* (9.4); *F. hodgsonii* (10.0); *F. hyperythra* (8.2); *F. hypoleuca* (13.9); *F. monileger* (11.0); *F. mugimaki* (11.7); *F. narcissina* (13.1); *F. nigrorufa* (8.5); *F. parva* (9.9); *F. sapphira* (7.8); *F. solitaris* (10.0); *F. semitorquata* (14.0); *F. strophiata* (13.0); *F. subrubra* (10.4); *F. superciliaris* (8.0); *F. tricolor* (8.5); *F. westermanni* (7.8); *F. zanthopygia* (12.2); *Fraseria cinerascens* (23.1); *F. ocreata* (35.5); *Grandala coelicolor* (45.6); *Hodgsonius phaenicuroides* (21.1); *Irania gutturalis* (21.6); *Luscinia brunnea* (17.5); *L. calliope* (18.5); *L. cyane* (14.8); *L. luscinia* (23.8); *L. megarhynchos* (19.6); *L. obscura* (12.0); *L. pectardens* (16.7); *L. pectoralis* (23.4); *L. ruficeps* (18.0); *L. sibilans* (16.7); *L. svecica* (17.8); *Melaenornis annamarulae* (39.9); *M. ardesiacus* (29.0); *M. brunneus* (25.3); *M. chocolatinus* (23.4); *M. edolioides* (30.7); *M. fischeri* (23.8); *M. infuscatus* (37.0); *M. mariquensis* (25.2); *M. microrhynchus* (19.4); *M. pallidus* (24.7); *M. pammelaina* (30.2); *M. silens* (26.2); *Modulatrix stictigula* (22.5); *Monticola angolensis* (44.4); *M. brevipes* (33.0); *M. cinclorhynchus* (36.0); *M. explorator* (55.0); *M. gularis* (34.6); *M. rufiventris* (62.1); *M. rufocinereus* (24.0); *M. ruperstris* (53.2); *M. saxatilis* (50.3); *M. solitarius* (50.5); *Muscicapa adusta* (10.4); *M. aquatica* (11.5); *M. boehmi* (15.4); *M. caerulescens* (17.6); *M. cassini* (17.3); *M. comitata* (14.1); *M. dauurica* (9.8); *M. epulata* (9.6); *M. ferruginea* (12.0); *M. gambagae* (13.0); *M. griseisticta* (15.9); *M. infuscata* (17.7); *M. lendu* (14.2); *M. muttui* (12.0); *M. olivascens* (15.6); *M. ruficauda* (13.3); *M. sethsmithi* (9.1); *M. sibirica* (13.2); *M. striata* (15.9); *M. tessmanni* (15.4); *M. ussheri* (17.9); *Muscicapella hodgsoni* (9.8); *Myioparus griseigularis* (13.4); *M. plumbeus* (12.8); *Myiophonus caeruleus* (158.0); *M. horsfieldii* (117.0); *M. robinsoni* (99.2); *Myrmecocichla aethiops* (56.6); *M. albifrons* (20.6); *M. arnotti* (39.6); *M. cinnamomeiventris* (39.6); *M. formicivora* (41.6); *M. melaena* (38.8); *M. nigra* (40.3); *M. semirufa* (34.2); *M. tholloni* (42.2); *Namibornis herero* (27.2); *Neocossyphus finschii* (37.0); *N. fraseri* (35.7); *N. poensis* (51.8); *N. rufus* (65.9); *Niltava davidi* (22.0); *N. grandis* (30.3); *N. macgrigoriae* (12.0); *N. sumatrana* (19.0); *N. sundara* (21.1); *N. vivida* (33.0); *Oenanthe alboniger* (25.2); *O. bottae* (19.9); *O. deserti* (19.9); *O. finschii* (27.5); *O. hispanica* (15.1); *O. isabellina* (29.4); *O. leucopyga* (27.9); *O. leucura* (41.0); *O. lugens* (22.5); *O. lugentoides* (22.5); *O. moesta* (30.2); *O. monacha* (21.6); *O. monticola* (33.1); *O. oenanthe* (26.9); *O. phillipsi* (20.0); *O. picata* (21.8); *O. pileata* (26.8); *O. pleschanka* (19.4); *O. xanthoprymna* (22.7); *Pinarornis plumosus* (65.8); *Pogonocichla stellata* (18.6); *Psophocichla litsitsirupa* (74.0); *Rhinomyias brunneata* (17.0); *R. olivacea* (15.7); *R. umbratilis* (18.2); *Rhyacornis fuliginosus* (20.4); *Saxicola bifasciata* (35.6); *S. caprata* (15.2); *S. ferrea* (14.8); *S. insignis* (15.0); *S. jerdoni* (14.8); *S. leucura* (12.6); *S. macrorhyncha* (15.0); *S. rubetra* (16.6); *S. torquata* (15.0); *Saxicoloides fulicata* (16.6); *Sheppardia aequatorialis* (16.8); *S. bocagei* (18.5); *S. cyornithopsis* (18.4); *S. gabela* (11.0); *S. gunningi* (17.4); *S. lowei* (18.4); *S. montana* (21.8); *S. sharpei* (14.7); *Stenostira scita* (5.9); *Stiphrornis erythrothorax* (15.6); *Swynnertonia swynnertonia* (31.4); *Tarsiger chrysaeus* (13.8); *T. cyanurus* (13.5);

T. hyperythrus (12.0); *T. indicus* (14.6); *Trichixos pyrropyga* (40.9); *Turdus albicollis* (54.0); *T. albocinctus* (99.4); *T. amaurochalinus* (57.9); *T. assimilis* (70.2); *T. boulboul* (97.1); *T. cardis* (39.3); *T. chiguanco* (93.3); *T. daguae* (72.0); *T. dissimilis* (75.0); *T. falcklandii* (93.9); *T. feae* (71.0); *T. fulviventris* (70.0); *T. fumigatus* (75.9); *T. fuscater* (143.0); *T. grayi* (79.5); *T. haplochrous* (84.0); *T. hauxwelli* (69.0); *T. hortulorum* (66.7); *T. ignobilis* (63.9); *T. iliacus* (61.2); *T. infuscatus* (72.4); *T. kessleri* (92.2); *T. lawrencii* (72.6); *T. leucomelas* (69.1); *T. libonyanus* (60.6); *T. maculirostris* (69.6); *T. maranonicus* (70.0); *T. menachensis* (75.5); *T. merula* (103.0); *T. migratorius* (78.5); *T. mupinensis* (62.7); *T. naumanni* (77.9); *T. nigrescens* (96.0); *T. nigriceps* (52.7); *T. nudigenis* (63.9); *T. obscurus* (62.6); *T. obsoletus* (74.8); *T. olivaceus* (72.1); *T. olivater* (86.7); *T. pallidus* (72.1); *T. pelios* (65.4); *T. philomelos* (67.8); *T. pilaris* (106.0); *T. plebejus* (86.5); *T. reevei* (61.0); *T. rubrocanus* (92.2); *T. ruficollis* (83.0); *T. rufitorques* (72.0); *T. rufiventris* (69.5); *T. rufopalliatus* (76.8); *T. serranus* (84.9); *T. subalaris* (49.5); *T. tephronotus* (49.4); *T. torquatus* (111.0); *T. unicolor* (64.2); *T. viscivorus* (118.0); *Xenocopsychus ansorgei* (35.5); *Zoothera cameronensis* (44.0); *Z. citrina* (53.3); *Z. crossleyi* (72.0); *Z. dauma* (104.0); *Z. dixoni* (90.0); *Z. gurneyi* (57.9); *Z. guttata* (57.5); *Z. interpres* (51.2); *Z. marginata* (81.0); *Z. mollissima* (98.2); *Z. monticola* (126.0); *Z. oberlaenderi* (43.4); *Z. piaggiae* (51.1); *Z. princei* (65.4); *Z. sibirica* (75.5); *Z. wardii* (58.6); *Corythaeola cristata* (965.0); *Corythaixoides concolor* (258.0); *C. personata* (250.0); *Crinifer piscator* (370.0); *C. zonurus* (527.0); *Criniferoides leucogaster* (203.0); *Musophaga johnstoni* (240.0); *M. porphyreolopha* (278.0); *M. rossae* (375.0); *M. violacea* (360.0); *Tauraco bannermani* (224.0); *T. erythrolophus* (268.0); *T. fischeri* (250.0); *T. hartlaubi* (224.0); *T. leucolophus* (219.0); *T. leucotis* (265.0); *T. macrorhynchus* (245.0); *T. persa* (306.0); *T. ruspolii* (263.0); *T. schuetti* (235.0); *Aethopyga christinae* (5.2); *A. gouldiae* (6.2); *A. ignicauda* (8.2); *A. mystacalis* (6.0); *A. nipalensis* (6.3); *A. saturata* (5.3); *A. siparaja* (6.7); *Anabathmis reichenbachii* (11.4); *Anthobaphes violacea* (9.4); *Anthreptes anchietae* (8.0); *A. aurantium* (12.0); *A. gabonicus* (8.0); *A. longuemarei* (11.5); *A. malacensis* (11.4); *A. metallicus* (7.2); *A. neglectus* (11.9); *A. orientalis* (10.3); *A. rectirostris* (10.6); *A. reichenowi* (7.3); *A. rhodolaema* (13.1); *A. rubritorques* (10.7); *A. seimundi* (6.7); *A. simplex* (9.0); *A. singalensis* (8.6); *Arachnothera affinis* (26.4); *A. chrysogenys* (23.2); *A. crassirostris* (16.0); *A. flavigaster* (38.4); *A. longirostra* (12.6); *A. magna* (30.7); *A. robusta* (38.0); *Chalcomitra adelberti* (9.8); *C. amethystina* (13.7); *C. fuliginosa* (11.9); *C. hunteri* (11.8); *C. rubescens* (10.4); *C. senegalensis* (12.4); *Cinnyris afra* (11.2); *C. batesi* (6.3); *C. bifasciata* (7.2); *C. bouvieri* (8.7); *C. chalcomelas* (8.2); *C. chalybea* (7.8); *C. chloropygia* (7.1); *C. coccinigastra* (14.3); *C. congensis* (9.0); *C. cuprea* (8.5); *C. erythrocerca* (8.8); *C. fusca* (7.9); *C. habessinica* (9.6); *C. johannae* (13.1); *C. loveridgei* (9.8); *C. ludovicensis* (8.7); *C. manoensis* (9.5); *C. mariquensis* (11.5); *C. mediocris* (8.2); *C. minulla* (5.7); *C. moreani* (8.3); *C. nectarinioides* (4.8); *C. neergaardi* (6.2); *C. osea* (7.2); *C. oustaleti* (7.5); *C. pulchella* (7.1); *C. regia* (6.6); *C. reichenowi* (8.0); *C. rockefelleri* (5.3); *C. rufipennis* (8.8); *C. shelleyi* (9.1); *C. stuhlmanni* (6.5); *C. superba* (16.8); *C. talatala* (8.1); *C. tsavoensis* (6.8); *C. ursulae* (6.5); *C. venusta* (6.5); *Cyanomitra alinae* (12.6); *C. bannermani* (14.0); *C. cyanolaema* (16.8); *C. obscura* (10.5); *C. olivacea* (9.9); *C. oritis* (11.2); *C. veroxii* (11.5); *C. verticalis* (14.5); *Deleornis fraseri* (11.4); *Dicaeum agile* (9.0); *D. chrysorrheum* (9.0); *D. concolor* (6.5); *D. cruentatum* (6.6); *D. erythrorhynchos* (6.3); *D. everetti* (9.0); *D. hirundinaceum* (9.1); *D. ignipectus* (5.9); *D. melanoxanthum* (11.0); *D. trigonostigma* (7.1); *Hedydipna collaris* (7.0); *H. pallidigastra* (6.8); *H. platura* (6.7); *Hypogramma hypogrammicum* (11.5); *Nectarinia asiatica* (8.1); *N. bocagei* (14.8); *N. calcostetha* (8.6); *N. famosa* (14.6); *N. habenssinica* (12.0); *N. johnstoni* (15.2); *N. jugularis* (8.7); *N. kilimensis* (15.7); *N. lotenia* (8.5); *N. minima* (5.0); *N. purpureiventris* (11.5); *N. reichenowi* (14.7); *N. sperata* (6.4); *N. tacazze* (14.9); *N. zeylonica* (9.0); *Prionochilus maculatus* (7.8); *P. percussus* (8.9); *P. thoracicus* (8.9); *Promerops cafer* (34.9); *P. gurneyi* (35.0); *Dromococcyx pavoninus* (46.4); *D. phasianellus* (84.5); *Geococcyx californianus* (376.0); *G. velox* (180.0); *Morococcyx erythropygus* (64.6); *Neomorphus geoffroyi* (352.0); *N. pucheranii* (330.0); *N. radiolosus* (399.0); *N. rufipennis* (382.0); *Tapera naevia* (48.6); *Agelastes meleagrides* (815.0); *A. niger* (700.0); *Nyctibius aethereus* (441.0); *N. bracteatus* (52.0); *N. grandis* (547.0); *N. griseus* (173.0); *N. jamaicensis* (247.0); *N. leucopterus* (86.4); *N. maculosus* (173.0); *Callipepla californica* (163.0); *C. douglasii* (178.0); *C. gambelii* (166.0); *C. squamata* (184.0); *Colinus cristatus* (135.0); *C. leucopogon* (130.0); *C. nigrogularis* (130.0); *C. virginianus* (172.0); *Cyrtonyx montezumae* (1886.0); *C. ocellatus* (200.0); *Dactylortyx thoracicus* (205.0); *Dendrortyx barbatus* (432.0); *D. leucophrys* (369.0); *D. macroura* (431.0); *Odontophorus atrifrons* (304.0); *O. balliviani* (318.0); *O. capueira* (427.0); *O. columbianus* (340.0); *O. dialeucos* (260.0); *O. erythrops* (335.0); *O. gujanensis* (315.0); *O. guttatus* (304.0); *O. hyperythrus* (340.0); *O. leucolaemus* (295.0); *O. melanonotus* (322.0); *O. melanotis* (335.0); *O. speciosus* (317.0); *O. stellatus* (337.0); *O. strophium* (302.0); *Oreortyx pictus* (233.0); *Philortyx fascia-*

tus (130.0); *Rhynchortyx cinctus* (150.0); *Opisthocomus hoazin* (696.0); *Orthonyx spaldingii* (152.0); *O. temminckii* (58.2); *Ardeotis arabs* (6175.0); *A. australis* (4450.0); *A. kori* (8430.0); *A. nigriceps* (8188.0); *Chlamydotis undulata* (1555.0); *Eupodotis afra* (690.0); *E. caerulescens* (1366.0); *E. hartlaubii* (1550.0); *E. humilis* (698.0); *E. melanogaster* (2050.0); *E. rueppellii* (1110.0); *E. ruficrista* (714.0); *E. senegalensis* (775.0); *E. vigorsii* (1700.0); *Houboiropsis bengalensis* (2025.0); *Neotis denhami* (4828.0); *N. heuglinii* (4400.0); *N. ludwigii* (3438.0); *N. nuba* (5440.0); *Otis tarda* (7896.0); *Sypheotides indica* (625.0); *Tetrax tetrax* (834.0); *Pandion haliaetus* (1486.0); *Acanthiza apicalis* (7.5); *A. chrysorrhoa* (9.3); *A. inornata* (6.2); *A. iredalei* (6.1); *A. katherina* (7.2); *A. lineata* (6.4); *A. nana* (6.2); *A. pusilla* (7.5); *A. reguloides* (7.7); *A. robustirostris* (6.1); *A. uropygialis* (6.4); *Aphelocephala leucopsis* (12.4); *A. nigricincta* (10.4); *A. pectoralis* (9.0); *Calamanthus fuliginosus* (21.2); *Chthonicola sagittata* (8.0); *Dasyornis brachypterus* (41.8); *D. broadbenti* (67.9); *D. longirostris* (32.7); *Gerygone chloronotus* (6.6); *G. fusca* (5.4); *G. levigaster* (6.2); *G. magnirostris* (6.8); *G. mouki* (5.2); *G. olivacea* (6.8); *G. palpebrosa* (7.8); *G. tenebrosa* (7.7); *Oreoscopus gutturalis* (20.1); *Origma solitaria* (14.4); *Pardalotus punctatus* (8.7); *P. rubricatus* (10.9); *P. striatus* (11.4); *P. xanthopygus* (9.5); *Pycnoptilus floccosus* (29.0); *Pyrrholaemus brunneus* (12.5); *Sericornis beccarii* (10.9); *S. cautus* (18.0); *S. citreogularis* (17.7); *S. frontalis* (13.1); *S. keri* (11.4); *S. magnirostris* (9.8); *S. pyrrhopygius* (18.0); *Smicrornis brevirostris* (5.3); *G. sulphurea* (6.5); *Anthoscopus caroli* (6.9); *A. flavifrons* (8.0); *A. minutus* (6.6); *A. musculus* (5.2); *A. parvulus* (5.8); *A. punctifrons* (7.0); *Baeolophus atricristatus* (17.5); *B. bicolor* (21.6); *B. inornatus* (16.0); *B. ridgwayi* (15.7); *B. wollweberi* (10.4); *Cephalopyrus flammiceps* (7.0); *Cyanistes cyanus* (14.7); *C. flavipectus* (11.5); *Lophophanes cristatus* (11.1); *Melanochlora sultanea* (37.6); *Pardaliparus venustulus* (10.0); *Parus afer* (20.2); *P. albiventris* (21.2); *P. ater* (11.7); *P. bokharensis* (17.5); *P. caeruleus* (10.7); *P. carpi* (18.6); *P. cinctus* (12.4); *P. cinerascens* (20.0); *P. dichrous* (13.2); *P. fasciiventer* (15.2); *P. fringillinus* (13.0); *P. funereus* (25.6); *P. griseiventris* (15.5); *P. leucomelas* (16.1); *P. leuconotus* (16.8); *P. lugubris* (17.5); *P. major* (15.2); *P. melanolophus* (8.6); *P. montanus* (10.2); *P. monticolus* (14.3); *P. niger* (21.5); *P. nuchalis* (13.8); *P. palustris* (10.8); *P. rubidiventris* (11.9); *P. rufiventris* (18.2); *P. rufonuchalis* (12.7); *P. spilonotus* (18.8); *P. thruppi* (12.0); *P. xanthogenys* (14.9); *Pholidornis rushiae* (6.0); *Poecile atricapilla* (10.8); *P. carolinensis* (10.0); *P. davidi* (10.3); *P. gambeli* (11.1); *P. hudsonica* (9.8); *P. rufescens* (9.4); *P. sclateri* (10.1); *P. superciliosa* (10.7); *Remiz consobrinus* (9.1); *R. coronatus* (6.9); *R. pendulinus* (9.3); *Sittiparus varius* (17.0); *Sylviparus modestus* (7.3); *Amadina erythrocephala* (22.5); *A. fasciata* (17.9); *Amandava amandava* (9.0); *A. formosa* (9.0); *A. subflava* (7.5); *Amblyospiza albifrons* (32.0); *Anaplectes rubriceps* (22.6); *Anomalospiza imberbis* (20.6); *Anthus bogotensis* (25.1); *A. brachyurus* (15.3); *A. caffer* (16.8); *A. campestris* (23.0); *A. cervinus* (20.9); *A. chacoensis* (26.0); *A. chloris* (25.1); *A. correndera* (20.9); *A. crenatus* (30.7); *A. furcatus* (20.3); *A. godlewskii* (25.4); *A. gustavi* (19.8); *A. hellmayri* (18.8); *A. hodgsoni* (21.3); *A. hoeschi* (27.0); *A. leucophrys* (25.1); *A. lineiventris* (35.0); *A. lutescens* (14.1); *A. melindae* (22.5); *A. nattereri* (19.5); *A. nilghiriensis* (31.0); *A. novaeseelandiae* (24.0); *A. pallidiventris* (32.0); *A. petrosus* (22.4); *A. pratensis* (18.4); *A. richardi* (32.2); *A. roseatus* (21.0); *A. rubescens* (20.7); *A. rufulus* (20.6); *A. similis* (25.3); *A. sokokensis* (15.0); *A. spinoletta* (23.9); *A. spragueii* (25.5); *A. sylvanus* (31.0); *A. trivialis* (23.4); *A. vaalensis* (27.0); *Brachycope anomala* (25.3); *Bubalornis albirostris* (71.0); *B. niger* (76.4); *Clytospiza monteiri* (14.9); *Coccopygia melanotis* (7.3); *C. quartinia* (7.0); *Cryptospiza jacksoni* (13.0); *C. reichenowii* (12.4); *C. salvadorii* (12.2); *C. shelleyi* (17.6); *Dendronanthus indicus* (16.4); *Dinemellia dinemelli* (63.9); *Emblema pictum* (10.4); *Erythrura gouldiae* (16.5); *E. hyperythra* (11.0); *E. prasina* (11.2); *E. trichroa* (14.4); *Estrilda astrild* (8.3); *E. atricapilla* (7.8); *E. caerulescens* (9.4); *E. charmosyna* (7.4); *E. erytronotos* (9.2); *E. kandti* (7.8); *E. melpoda* (7.6); *E. nigriloris* (8.5); *E. nonnula* (7.7); *E. paludicola* (7.6); *E. perreini* (7.4); *E. poliopareia* (9.9); *E. rhodopyga* (7.7); *E. rufibarba* (8.5); *E. thomensis* (7.6); *E. troglodytes* (7.6); *Euodice cantans* (11.9); *Euplectes afer* (14.3); *E. albonotatus* (21.2); *E. ardens* (19.2); *E. aureus* (16.0); *E. axillaris* (25.3); *E. capensis* (30.6); *E. diadematus* (13.9); *E. franciscamus* (16.0); *E. gierowii* (28.3); *E. hartlaubi* (16.0); *E. hordeaceus* (19.4); *E. jacksoni* (37.5); *E. macroura* (21.9); *E. nigroventris* (12.5); *E. orix* (23.1); *E. progne* (35.1); *E. psammocromius* (35.5); *Euschistospiza cinereovinacea* (12.0); *E. dybowskii* (13.4); *Granatina granatina* (11.7); *G. ianthinogaster* (14.7); *Heteromunia pectoralis* (15.2); *Histurgops ruficaudus* (69.0); *Hypargos margaritatus* (12.8); *H. niveoguttatus* (14.6); *Lagonosticta larvata* (9.9); *L. nitidula* (10.7); *L. rara* (10.4); *L. rhodopareia* (9.3); *L. rubricata* (10.2); *L. rufopicta* (9.3); *L. sanguinodorsalis* (11.4); *L. senegala* (9.3); *L. umbrinodorsalis* (10.4); *L. virata* (9.3); *Lonchura castaneothorax* (10.5); *L. flaviprymna* (11.7); *L. kelaarti* (14.1); *L. leucogastra* (11.4); *L. maja* (12.5); *L. malabarica* (12.0); *L. malacca* (12.0); *L. punctulata* (13.6); *L. striata* (12.3); *Macronyx ameliae* (33.5); *M. aurantiigula* (39.4); *M. capensis* (50.1); *M. croceus* (47.1); *M. flavicol-*

lis (33.0); *M. fuelleborni* (55.3); *M. grimwoodi* (60.0); *M. sharpei* (28.0); *Malimbus ballmanni* (32.0); *M. cassini* (31.0); *M. coronatus* (32.0); *M. erythrogaster* (37.0); *M. ibadanensis* (39.0); *M. malimbicus* (36.2); *M. nitens* (38.1); *M. racheliae* (30.0); *M. rubricollis* (42.2); *M. scutatus* (30.0); *Mandingoa nitidula* (9.6); *Montifringilla adamsi* (36.0); *M. blanfordi* (23.0); *M. davidiana* (21.2); *M. nivalis* (36.9); *M. ruficollis* (22.8); *M. taczanowskii* (36.0); *Motacilla aguimp* (27.0); *M. alba* (24.0); *M. capensis* (20.8); *M. cinerea* (17.0); *M. citreola* (19.2); *M. clara* (17.9); *M. flava* (22.5); *M. lugens* (20.0); *M. lutea* (15.0); *M. madaraspatensis* (30.5); *Neochmia modesta* (12.8); *N. phaeton* (10.0); *N. ruficauda* (11.2); *N. temporalis* (11.4); *Nesocharis ansorgei* (8.4); *N. capistrata* (11.6); *N. shelleyi* (7.6); *Nigrita bicolor* (10.5); *N. canicapillus* (18.7); *N. fusconotus* (9.1); *N. luteifrons* (13.2); *Odontospiza griseicapilla* (15.1); *Ortygospiza atricollis* (10.6); *O. fuscocrissa* (11.0); *O. gabonensis* (11.0); *Pachyphantes superciliosus* (21.4); *Paludipasser locustella* (16.0); *Parmoptila jamesoni* (9.5); *P. rubrifrons* (9.5); *P. woodhousei* (9.4); *Passer ammodendri* (29.0); *P. castanopterus* (18.0); *P. cordofanicus* (18.5); *P. diffusus* (24.2); *P. domesticus* (26.0); *P. eminibey* (13.4); *P. euchlorus* (14.0); *P. flaveolus* (18.5); *P. gongonensis* (39.9); *P. griseus* (28.4); *P. hispaniolensis* (24.2); *P. luteus* (13.0); *P. melanurus* (29.5); *P. moabiticus* (16.5); *P. montanus* (21.4); *P. motitensis* (30.5); *P. pyrrhonotus* (19.0); *P. rufocinctus* (27.8); *P. rutilans* (18.5); *P. shelleyi* (18.5); *P. simplex* (19.5); *P. suahelicus* (30.0); *P. swainsonii* (31.6); *Petronia brachydactyla* (25.0); *P. dentata* (18.4); *P. petronia* (30.2); *P. pyrgita* (24.1); *P. superciliaris* (24.0); *P. xanthocollis* (18.1); *Philetairus socius* (27.4); *Plocepasser donaldsoni* (39.9); *P. mahali* (41.6); *P. rufoscapulatus* (44.6); *P. superciliosus* (37.1); *Ploceus albinucha* (27.2); *P. alientus* (22.2); *P. angolensis* (19.0); *P. aurantius* (23.0); *P. aureonucha* (18.0); *P. badius* (24.0); *P. baglafecht* (31.6); *P. bannermani* (30.8); *P. batesi* (24.0); *P. benghalensis* (19.8); *P. bertrandi* (39.1); *P. bicolor* (34.2); *P. bojeri* (22.6); *P. burnieri* (18.1); *P. capensis* (44.2); *P. castaneiceps* (18.5); *P. castanops* (21.5); *P. cucullatus* (36.4); *P. dicrocephalus* (18.5); *P. dorsomaculatus* (24.0); *P. flavipes* (28.0); *P. galbula* (19.6); *P. golandi* (23.6); *P. hypoxanthus* (18.6); *P. insignis* (27.5); *P. intermedius* (20.6); *P. jacksoni* (23.6); *P. katangae* (19.0); *P. luteolus* (15.1); *P. manyar* (17.4); *P. megarhynchus* (34.5); *P. melannocephalus* (23.3); *P. melanogaster* (22.4); *P. nicolli* (29.9); *P. nigerrimus* (34.5); *P. nigricollis* (27.1); *P. nigrimentum* (27.0); *P. ocularis* (25.2); *P. olivaceiceps* (21.1); *P. pelzelni* (15.3); *P. philippinus* (28.2); *P. preussi* (31.6); *P. reichardi* (25.5); *P. rubiginosus* (30.1); *P. ruweti* (19.0); *P. spekei* (35.2); *P. spekeoides* (25.0); *P. subaureus* (30.7); *P. subpersonatus* (12.5); *P. taeniopterus* (17.7); *P. temporalis* (35.8); *P. tricolor* (38.2); *P. velatus* (31.1); *P. vitellinus* (20.0); *P. weynsi* (29.1); *P. xanthops* (40.8); *P. xanthopterus* (22.2); *Poephila acuticauda* (14.0); *P. cincta* (14.9); *P. personata* (13.0); *Prunella atrogularis* (18.5); *P. collaris* (37.1); *P. fagani* (21.9); *P. fulvescens* (18.9); *P. himalayana* (26.7); *P. immaculata* (20.7); *P. koslowi* (30.0); *P. modularis* (20.3); *P. montanella* (17.0); *P. ocularis* (22.5); *P. rubeculoides* (24.0); *P. strophiata* (18.2); *Pseudonigrita arnaudi* (20.0); *P. cabanisi* (20.7); *Pyrenestes minor* (20.0); *P. ostrinus* (22.5); *P. sanguineus* (19.2); *Pytilia afra* (16.6); *P. hypogrammica* (14.8); *P. lineata* (14.3); *P. melba* (15.4); *P. phoenicoptera* (14.5); *Quelea cardinalis* (12.7); *Q. erythrops* (19.4); *Q. quelea* (18.6); *Spermestes bicolor* (11.0); *S. cucullatus* (10.0); *S. fringilloides* (16.5); *Spermophaga haematina* (23.0); *S. poliogenys* (19.8); *S. ruficapilla* (23.6); *Sporopipes frontalis* (17.3); *S. squamifrons* (12.3); *Stagonopleura bella* (14.0); *S. guttata* (17.6); *S. oculata* (12.9); *Taeniopygia bichenovii* (9.6); *T. guttata* (12.1); *Tmetothylacus tenellus* (20.1); *Uraeginthus angolensis* (9.9); *U. bengalus* (9.9); *U. cyanocephalus* (9.8); *Vidua camerunensis* (12.1); *V. chalybeata* (12.5); *V. codringtoni* (12.8); *V. fischeri* (12.3); *V. funerea* (14.4); *V. hypocherina* (11.9); *V. interjecta* (20.6); *V. larvaticola* (13.1); *V. macroura* (15.8); *V. maryae* (12.8); *V. nigeriae* (12.1); *V. obtusa* (20.8); *V. orientalis* (18.7); *V. paradisaea* (20.4); *V. purpurascens* (13.1); *V. raricola* (12.1); *V. regia* (14.4); *V. togoensis* (20.5); *V. wilsoni* (13.1); *Pedionomus torquatus* (63.2); *Balaeniceps rex* (5984.0); *Pelecanus conspicillatus* (5505.0); *P. crispus* (9550.0); *P. erythrorhynchos* (5650.0); *P. onocrotalus* (9520.0); *P. philippensis* (5025.0); *P. rufescens* (5445.0); *Phalacrocorax africanus* (645.0); *P. aristotelis* (1773.0); *P. atriceps* (2491.0); *P. auritus* (1817.0); *P. brasilianus* (1245.0); *P. carbo* (2571.0); *P. fuscicollis* (706.0); *P. melanoleucos* (734.0); *P. niger* (427.0); *P. pygmaeus* (679.0); *P. sulcitrostris* (1000.0); *P. varius* (1956.0); *Acryllium vulturinum* (1330.0); *Afropavo congrensis* (1281.0); *Alectoris barbara* (419.0); *A. chukar* (504.0); *A. graeca* (615.0); *A. magna* (554.0); *A. melanocephala* (623.0); *A. philbyi* (441.0); *A. rufa* (528.0); *Ammoperdix griseogularis* (204.0); *A. heyi* (190.0); *Arborophila atrogularis* (238.0); *A. brunneopectus* (268.0); *A. cambodiana* (288.0); *A. charltonii* (270.0); *A. chloropus* (270.0); *A. davidi* (241.0); *A. gingica* (253.0); *A. mandellii* (268.0); *A. orientalis* (336.0); *A. rufipectus* (403.0); *A. rufogularis* (351.0); *A. torqueola* (351.0); *Argusianus argus* (1994.0); *Bambusicola fytchii* (268.0); *B. thoracica* (270.0); *Bonasa bonasia* (429.0); *B. umbellus* (532.0); *Caloperdix oculea* (210.0); *Catreus wallichii* (1447.0); *Centrocercus minimus* (1650.0); *C.*

urophasianus (2209.0); *Chrysolophus amherstiae* (739.0); *C. pictus* (576.0); *Coturnix chinensis* (41.8); *C. coromandelica* (74.5); *C. coturnix* (96.5); *C. delegorguei* (76.0); *C. japonica* (94.8); *C. pectoralis* (102.0); *C. ypsilophora* (109.0); *Crossoptilon auritum* (1785.0); *C. crossoptilon* (2138.0); *C. harmani* (1705.0); *C. mantchuricum* (1901.0); *Dendragapus falcipennis* (688.0); *D. obscurus* (1059.0); *Falcipennis canadensis* (474.0); *Francolinus adspersus* (430.0); *F. afer* (482.0); *F. africanus* (391.0); *F. ahantensis* (548.0); *F. albogularis* (276.0); *F. bicalcaratus* (444.0); *F. camerunensis* (551.0); *F. capensis* (653.0); *F. castaneicollis* (829.0); *F. clappertoni* (474.0); *F. coqui* (259.0); *F. erckelii* (1200.0); *F. finschi* (570.0); *F. francolinus* (453.0); *F. griseostriatus* (307.0); *F. gularis* (510.0); *F. hartlaubi* (243.0); *F. harwoodi* (496.0); *F. hildebrandti* (539.0); *F. icterorhynchus* (506.0); *F. jacksoni* (1097.0); *F. lathami* (269.0); *F. leucoscepus* (649.0); *F. levaillantii* (432.0); *F. levaillantoides* (380.0); *F. nahani* (279.0); *F. natalensis* (516.0); *F. nobilis* (757.0); *F. ochropectus* (707.0); *F. pictus* (291.0); *F. pintadeanus* (339.0); *F. pondicerianus* (251.0); *F. psilolaemus* (480.0); *F. rufopictus* (718.0); *F. schlegelii* (237.0); *F. sephaena* (342.0); *F. shelleyi* (488.0); *F. squamatus* (458.0); *F. streptophorus* (385.0); *F. swainsonii* (606.0); *F. swierstrai* (470.0); *Galloperdix lunulata* (256.0); *G. spadicea* (369.0); *Gallus gallus* (904.0); *G. sonneratii* (855.0); *Guttera plumifera* (875.0); *G. pucherani* (1232.0); *Ithaginis cruentus* (538.0); *Lagopus lagopus* (587.0); *L. leucurus* (355.0); *L. mutus* (536.0); *Lerwa lerwa* (582.0); *Lophophorus impejanus* (2078.0); *L. lhuysii* (3008.0); *L. sclateri* (2348.0); *Lophura diardi* (1128.0); *L. edwardsi* (1082.0); *L. erythrophthalma* (940.0); *L. hatinhensis* (1100.0); *L. ignita* (1815.0); *L. imperialis* (1800.0); *L. leucomelanos* (1825.0); *L. nycthemera* (1490.0); *Melanoperdix nigra* (280.0); *Meleagris gallopavo* (7400.0); *M. ocellata* (4575.9); *Numida meleagris* (1299.0); *Ophrysia superciliosa* (705.0); *Pavo cristatus* (4194.0); *P. muticus* (2768.0); *Perdicula argoondah* (60.5); *P. asiatica* (69.5); *P. erythrorhyncha* (68.8); *P. manipurensis* (71.0); *Perdix dauurica* (264.0); *P. hodgsoniae* (372.0); *P. perdix* (406.0); *Phasianus colchicus* (1135.0); *Polyplectron bicalcaratum* (519.0); *P. germaini* (454.0); *P. inopinatum* (550.0); *P. malacense* (608.0); *Ptilopachus petrosus* (193.0); *Pucrasia macrolopha* (1058.0); *Rheinardia ocellata* (1900.0); *Rhizothera longirostris* (749.0); *Rollulus rouloul* (217.0); *Syrmaticus ellioti* (1017.0); *S. humiae* (889.0); *S. reevesii* (1239.0); *Tetrao mlokosiewiczi* (816.0); *T. parvirostris* (2958.0); *T. tetrix* (1083.0); *T. urogallus* (2950.0); *Tetraogallus altaicus* (2770.0); *T. caspius* (2514.0); *T. caucasicus* (1834.0); *T. himalayensis* (2428.0); *T. tibetanus* (1505.0); *Tetraophasis obscurus* (859.0); *T. szechenyii* (1070.0); *Tetrastes sewerzowi* (500.0); *Tragopan blythii* (1250.0); *T. caboti* (1150.0); *T. melanocephalus* (1650.0); *T. satyra* (1475.0); *T. temminckii* (1184.0); *Tympanuchus cupido* (876.0); *T. pallidicinctus* (746.0); *T. phasianellus* (885.0); *Phoenicoparrus andinus* (4900.0); *P. jamesi* (2000.0); *Phoenicopterus chilensis* (2277.0); *P. minor* (1500.0); *P. ruber* (3066.0); *Phoeniculus bollei* (54.6); *P. castaneiceps* (24.4); *P. damarensis* (81.9); *P. minor* (29.0); *P. purpureus* (74.3); *P. somaliensis* (26.5); *Phoenicurus alaschanicus* (17.5); *P. auroreus* (16.2); *P. caeruleocephalus* (14.9); *P. erythrogaster* (24.6); *P. erythronota* (18.5); *P. frontalis* (16.1); *P. hodgsoni* (17.2); *P. moussieri* (14.9); *P. ochruros* (16.5); *P. phoenicurus* (14.6); *P. schisticeps* (18.1); *Chaetops frenatus* (55.1); *C. pycnopygius* (28.3); *Picathartes gymnocephalus* (196.0); *P. oreas* (220.0); *Blythipicus pyrrhotis* (132.0); *B. rubiginosus* (82.3); *Campephilus gayaquilensis* (241.5); *C. guatemalensis* (255.0); *C. haematogaster* (237.0); *C. imperialis* (511.0); *C. leucopogon* (237.0); *C. magellanicus* (319.5); *C. melanoleucos* (250.0); *C. pollens* (246.1); *C. robustus* (200.0); *C. rubricollis* (205.0); *Campethera abingoni* (68.5); *C. bennettii* (70.1); *C. cailliautii* (41.1); *C. caroli* (42.5); *C. maculosa* (54.0); *C. nivosa* (37.8); *C. notata* (62.0); *C. nubica* (59.7); *C. punctuligera* (71.8); *C. tullbergi* (50.5); *Celeus brachyurus* (108.0); *C. castaneus* (100.0); *C. elegans* (127.0); *C. flavescens* (150.0); *C. flavus* (105.0); *C. grammicus* (67.0); *C. loricatus* (83.0); *C. lugubris* (143.0); *C. spectabilis* (111.0); *C. torquatus* (120.0); *C. undatus* (64.0); *Chrysocolaptes festivus* (213.0); *C. lucidus* (142.0); *Chrysoptilus atricollis* (113.7); *C. melanochloros* (256.0); *C. punctigula* (65.0); *Colaptes auratus* (134.0); *C. campestris* (158.0); *C. chrysoides* (111.0); *C. pitius* (159.0); *C. rupicola* (174.0); *Dendrocopos assimilis* (53.0); *D. atratus* (47.0); *D. auriceps* (40.0); *D. canicapillus* (22.8); *D. cathpharius* (31.0); *D. darjellensis* (71.0); *D. dorae* (19.5); *D. himalayensis* (68.0); *D. hyperythrus* (47.5); *D. kizuki* (19.2); *D. leucopterus* (67.0); *D. leucotos* (115.0); *D. macei* (45.3); *D. mahrattensis* (34.3); *D. major* (76.2); *D. medius* (59.0); *D. minor* (19.8); *D. moluccensis* (16.3); *D. nanus* (14.0); *D. syriacus* (76.8); *Dendrocopus kizuki* (15.0); *Dendropicos abyssinicus* (24.5); *D. elachus* (19.0); *D. elliotii* (37.2); *D. fuscescens* (26.0); *D. gabonensis* (26.0); *D. goertae* (44.6); *D. griseocephalus* (41.0); *D. namaquus* (82.5); *D. poecilolaemus* (28.1); *D. pyrrhogaster* (68.5); *D. stierlingi* (28.0); *D. xantholophus* (82.5); *Dinopium benghalense* (100.0); *D. javanense* (72.9); *D. rafflesii* (102.0); *D. shorii* (101.0); *Dryocopus galeatus* (124.0); *D. javensis* (272.0); *D. lineatus* (184.0); *D. martius* (321.0); *D. pileatus* (288.0); *D. schulzi* (200.0); *Gecinulus grantia* (76.5); *G. viridis* (70.5); *Geocolaptes olivaceus* (120.0); *Hemicircus canente*

(43.5); *H. concretus* (29.5); *Jynx ruficollis* (52.6); *J. torquilla* (29.2); *Leuconerpes candidus* (22.5); *Meiglyptes jugularis* (53.5); *M. tristis* (31.7); *M. tukki* (53.1); *Melanerpes aurifrons* (80.9); *M. cactorum* (35.1); *M. carolinus* (69.6); *M. chrysauchen* (52.8); *M. chrysogenys* (67.9); *M. cruentatus* (58.1); *M. erythrocephalus* (71.6); *M. flavifrons* (58.0); *M. formicivorus* (79.7); *M. hoffmannii* (73.0); *M. hypopolius* (52.4); *M. lewis* (106.0); *M. pucherani* (62.5); *M. pulcher* (60.0); *M. pygmaeus* (38.9); *M. rubricapillus* (52.5); *M. uropygialis* (64.9); *Mulleripicus pulverulentus* (462.0); *Picoides albolarvatus* (61.1); *P. arcticus* (69.3); *P. arizonae* (46.8); *P. borealis* (48.0); *P. lignarius* (34.0); *P. mixtus* (28.8); *P. nuttallii* (37.4); *P. obsoletus* (18.6); *P. pubescens* (25.3); *P. scalaris* (32.0); *P. stricklandi* (35.9); *P. tridactylus* (65.7); *P. villosus* (97.9); *Piculus aeruginosus* (75.0); *P. auricularis* (65.4); *P. aurulentus* (75.0); *P. callopterus* (68.9); *P. chrysochloros* (88.0); *P. flavigula* (55.0); *P. leucolaemus* (69.0); *P. litae* (69.0); *P. rivolii* (102.0); *P. rubiginosus* (55.8); *P. simplex* (55.0); *Picumnus albosquamatus* (11.9); *P. aurifrons* (8.9); *P. castelnau* (11.4); *P. cinnamomeus* (12.0); *P. cirratus* (10.2); *P. dorbigyanus* (9.6); *P. exilis* (9.3); *P. fulvescens* (11.1); *P. fuscus* (11.1); *P. granadensis* (12.2); *P. innominatus* (11.1); *P. lafresnayi* (9.5); *P. limae* (10.8); *P. minutissimus* (13.3); *P. nebulosus* (11.6); *P. nigropunctatus* (11.3); *P. olivaceus* (10.6); *P. pumilis* (9.5); *P. pygmaeus* (11.0); *P. rufiventris* (21.0); *P. sclateri* (11.1); *P. spilogaster* (13.2); *P. squamulatus* (10.2); *P. steindachneri* (9.9); *P. subtilis* (10.4); *P. temminckii* (11.5); *P. varzeae* (12.5); *Picus canus* (137.0); *P. chlorolophus* (65.8); *P. erythropygius* (118.0); *P. flavinucha* (178.0); *P. mentalis* (102.0); *P. mineaceus* (97.3); *P. puniceus* (79.1); *P. rabieri* (128.0); *P. squamatus* (170.0); *P. viridanus* (113.0); *P. viridis* (176.0); *P. vittatus* (110.0); *P. xanthopygaeus* (99.7); *Reinwardtipicus validus* (149.0); *Sasia abnormis* (9.2); *S. africana* (9.4); *S. ochracea* (9.7); *Sphyrapicus nuchalis* (47.9); *S. ruber* (53.5); *S. thyroideus* (47.6); *S. varius* (50.3); *Veniliornis affinis* (34.9); *V. callonotus* (26.6); *V. cassini* (34.6); *V. chocoensis* (30.0); *V. dignus* (37.6); *V. frontalis* (36.7); *V. fumigatus* (36.2); *V. kirkii* (28.8); *V. maculifrons* (31.4); *V. nigriceps* (44.0); *V. passerinus* (32.1); *V. sanguineus* (26.5); *V. spilogaster* (40.3); *Pitta angolensis* (65.5); *P. brachyura* (55.5); *P. caerulea* (202.0); *P. cyanea* (110.0); *P. elliotii* (91.0); *P. erythrogaster* (74.1); *P. granatina* (55.4); *P. guajana* (81.5); *P. gurneyi* (60.5); *P. iris* (62.2); *P. megarhyncha* (85.0); *P. moluccensis* (76.0); *P. nipalensis* (124.0); *P. nympha* (90.1); *P. oatesi* (120.0); *P. phayrei* (100.0); *P. reichenowi* (83.0); *P. sordida* (64.5); *P. soror* (114.0); *P. versicolor* (89.5); *Pluvianellus socialis* (84.3); *Podargus ocellatus* (174.0); *P. papuensis* (378.0); *P. strigoides* (302.0); *Aechmophorus clarkii* (961.0); *A. occidentalis* (1156.0); *Podiceps andinus* (297.0); *P. auritus* (453.0); *P. cristatus* (771.0); *P. gallardoi* (575.0); *P. grisegena* (1023.0); *P. major* (1646.0); *P. nigricollis* (415.0); *P. occipitalis* (321.0); *P. taczanowskii* (392.0); *Podilymbus gigas* (699.0); *P. podiceps* (416.0); *Poliocephalus poliocephalus* (241.0); *Rollandia microptera* (70.6); *R. rolland* (336.0); *Tachybaptus dominicus* (127.0); *T. novaehollandiae* (219.0); *T. ruficollis* (213.0); *Pomatostomus halli* (41.8); *P. ruficeps* (57.8); *P. superciliosus* (41.0); *P. temporalis* (75.0); *Agapornis fischeri* (48.3); *A. lilianae* (37.3); *A. personata* (52.5); *A. pullaria* (39.3); *A. roseicollis* (54.5); *A. swinderniana* (40.0); *A. taranta* (57.5); *Alisterus scapularis* (233.0); *Amazona aestiva* (451.0); *A. albifrons* (206.0); *A. amazonica* (370.0); *A. autumnalis* (416.0); *A. barbadensis* (380.7); *A. brasiliensis* (270.0); *A. diadema* (417.5); *A. dufresniana* (623.0); *A. farinosa* (626.0); *A. festiva* (430.0); *A. finschi* (302.0); *A. kawalli* (473.4); *A. mercenaria* (340.0); *A. ochrocephala* (440.0); *A. oratrix* (517.0); *A. pretrei* (275.0); *A. rhodocorytha* (475.0); *A. tucumana* (260.0); *A. viridigenalis* (316.0); *A. xantholora* (217.0); *A. xanthops* (241.6); *Anodorhynchus glaucus* (798.0); *A. hyacinthinus* (1331.0); *A. leari* (940.0); *Aprosmictus erythropterus* (136.0); *Ara ambigua* (1300.0); *A. ararauna* (1125.0); *A. chloropterus* (1214.0); *A. glaucogularis* (784.0); *A. macao* (1015.0); *A. militaris* (1134.0); *A. rubrogenys* (468.0); *A. severa* (343.0); *Aratinga acuticaudata* (171.0); *A. astec* (76.9); *A. aurea* (84.7); *A. auricapilla* (130.0); *A. cactorum* (92.9); *A. canicularis* (85.0); *A. erythrogenys* (151.0); *A. finschi* (150.0); *A. holochlora* (138.0); *A. jandaya* (89.4); *A. leucophthalmus* (158.0); *A. mitrata* (249.0); *A. pertinax* (84.0); *A. rubritorquis* (212.0); *A. solstitialis* (121.0); *A. strenua* (208.0); *A. wagleri* (194.0); *A. weddellii* (108.0); *Barnardius barnardi* (133.5); *B. zonarius* (141.0); *Bolborhynchus ferrugineifrons* (31.9); *B. lineola* (56.2); *B. orbygnesius* (43.1); *Brotogeris chiriri* (61.6); *B. chrysopterus* (54.5); *B. cyanoptera* (56.0); *B. jugularis* (63.3); *B. pyrrhopterus* (64.0); *B. sanctithomae* (59.0); *B. tirica* (63.0); *B. versicolurus* (71.6); *Cacatua galerita* (724.0); *C. leadbeateri* (392.0); *C. pastinator* (666.0); *C. roseicapilla* (400.0); *C. tenuirostris* (567.0); *Callocephalon fimbriatum* (256.0); *Calyptorhynchus banksii* (724.0); *C. baudinii* (620.0); *C. funereus* (679.0); *C. lathami* (437.0); *Cyanoliseus patagonus* (278.0); *Cyanopsitta spixii* (200.0); *Cyclopsitta diophthalma* (42.4); *Deroptyus accipitrinus* (240.0); *Diopsittaca nobilis* (151.0); *Eclectus roratus* (487.0); *Enicognathus ferrugineus* (160.0); *E. leptorhynchus* (193.0); *Forpus coelestis* (26.2); *F. conspicillatus* (26.4); *F. cyanopygius* (33.5); *F. passerinus* (23.0); *F. sclateri* (27.2); *F. xanthops* (33.4); *F. xanthopterygius* (31.0); *Geoffroyus geoffroyi*

(164.0); *Glossopsitta concinna* (70.8); *G. porphyrocephala* (44.7); *G. pusilla* (39.4); *Graydidascalus brachyurus* (159.0); *Guaruba guarouba* (194.0); *Hapalopsittaca amazonina* (106.0); *H. fuertesi* (105.0); *H. melanotis* (158.0); *H. pyrrhops* (103.0); *Leptosittaca branickii* (309.0); *Loriculus galgulus* (28.0); *L. vernalis* (35.7); *Melopsittacus undulatus* (29.0); *Myiopsitta monachus* (120.0); *Nandayus nenday* (128.0); *Nannopsittaca dachilleae* (41.5); *N. panychlora* (44.1); *Neophema chrysostoma* (45.9); *N. elegans* (43.4); *N. pulchella* (38.0); *N. splendida* (38.6); *Neopsephotus bourkii* (44.4); *Northiella haematogaster* (85.9); *Nymphicus hollandicus* (94.7); *Ognorhynchus icterotis* (285.0); *Orthopsittaca manilata* (372.0); *Pezoporus occidentalis* (200.0); *P. wallicus* (71.4); *Pionites leucogaster* (155.0); *P. melanocephala* (149.0); *Pionopsitta barrabandi* (140.0); *P. caica* (132.0); *P. haematotis* (149.0); *P. pileata* (119.0); *P. pulchra* (150.0); *P. pyrilia* (148.1); *P. vulturina* (148.1); *Pionus chalcopterus* (210.0); *P. fuscus* (206.0); *P. maximiliani* (293.0); *P. menstruus* (251.0); *P. senilis* (212.0); *P. seniloides* (210.0); *P. sordidus* (266.0); *P. tumultuosus* (239.0); *Platycercus adscitus* (111.0); *P. elegans* (125.0); *P. eximius* (104.0); *P. icterotis* (63.3); *P. venustus* (89.5); *Poicephalus crassus* (187.1); *P. cryptoxanthus* (140.0); *P. flavifrons* (174.0); *P. gulielmi* (275.0); *P. meyeri* (118.0); *P. robustus* (344.0); *P. rueppellii* (116.0); *P. rufiventris* (120.0); *P. senegalus* (147.0); *Polytelis alexandrae* (104.0); *P. anthopeplus* (170.0); *P. swainsonii* (153.0); *Probosciger aterrimus* (841.0); *Propyrrhura auricollis* (249.0); *P. couloni* (250.0); *P. maracana* (256.0); *Psephotus chrysopterygius* (46.8); *P. dissimilis* (45.8); *P. haematonotus* (61.4); *P. pulcherrimus* (61.5); *P. varius* (61.5); *Psilopsiagon aurifrons* (33.6); *P. aymara* (30.0); *Psittacula alexandri* (147.0); *P. columboides* (85.5); *P. cyanocephala* (66.0); *P. derbiana* (251.0); *P. eupatria* (214.0); *P. finschii* (89.6); *P. himalayana* (110.0); *P. krameri* (117.0); *P. longicauda* (107.0); *P. roseata* (66.0); *Psittacus erithacus* (402.0); *Psitteuteles versicolor* (53.5); *Psittinus cyanurus* (35.0); *Purpureicephalus spurius* (116.0); *Pyrrhura albipectus* (74.8); *P. anaca* (71.3); *P. caeruleiceps* (63.0); *P. calliptera* (72.5); *P. cruentata* (79.5); *P. devillei* (75.9); *P. egregia* (75.9); *P. eisenmanni* (63.0); *P. emma* (73.6); *P. frontalis* (80.1); *P. hoematotis* (68.7); *P. hoffmanni* (82.2); *P. lepida* (74.8); *P. leucotis* (71.3); *P. melanura* (70.6); *P. molinae* (77.1); *P. orcesi* (70.8); *P. perlata* (75.0); *P. pfrimeri* (71.3); *P. picta* (62.1); *P. rhodocephala* (75.4); *P. rupicola* (75.0); *P. subandina* (63.0); *P. viridicata* (74.8); *Rhynchopsitta pachyrhyncha* (325.0); *R. terrisi* (442.0); *Touit batavica* (55.0); *T. costaricensis* (80.0); *T. dilectissima* (65.0); *T. huetii* (60.0); *T. melanonota* (67.8); *T. purpurata* (59.7); *T. stictoptera* (78.8); *T. surda* (67.2); *Trichoglossus chlorolepidotus* (87.1); *T. haematodus* (117.2); *T. rubritorquis* (120.0); *Triclaria malachitacea* (152.0); *Psophia crepitans* (1026.0); *P. leucoptera* (1317.0); *P. viridis* (1071.0); *Pterocles alchata* (285.0); *P. bicinctus* (237.0); *P. burchelli* (181.0); *P. coronatus* (300.0); *P. decoratus* (184.0); *P. exustus* (212.0); *P. gutturalis* (338.0); *P. indicus* (179.0); *P. lichtensteinii* (211.0); *P. namaqua* (177.0); *P. orientalis* (406.0); *P. senegallus* (264.0); *Syrrhaptes paradoxus* (257.0); *S. tibetanus* (347.0); *Ailuroedus crassirostris* (206.0); *A. melanotis* (177.0); *Chlamydera cerviniventris* (157.0); *C. guttata* (136.0); *C. maculata* (140.0); *C. nuchalis* (201.0); *Prionodura newtoniana* (78.5); *Ptilonorhynchus violaceus* (219.0); *Scenopoeetes dentirostris* (164.0); *Sericulus chrysocephalus* (100.0); *Alophoixus finschii* (24.2); *A. flaveolus* (45.7); *A. ochraceus* (41.5); *A. pallidus* (46.0); *A. phaeocephalus* (32.0); *Andropadus ansorgei* (18.7); *A. curvirostris* (24.9); *A. gracilirostris* (31.3); *A. gracilis* (21.7); *A. importunus* (27.4); *A. latirostris* (26.3); *A. masukuensis* (26.8); *A. milanjensis* (37.4); *A. montanus* (32.6); *A. tephrolaemus* (38.3); *A. virens* (26.3); *Baeopogon clamans* (46.5); *B. indicator* (45.9); *Bleda canicapilla* (40.3); *B. eximia* (35.7); *B. syndactyla* (45.5); *Calyptocichla serina* (38.8); *Chlorocichla falkensteini* (31.7); *C. flavicollis* (48.8); *C. flaviventris* (39.5); *C. laetissima* (50.2); *C. prigoginei* (42.8); *C. simplex* (46.5); *Criniger barbatus* (42.6); *C. calurus* (36.2); *C. chloronotus* (45.0); *C. ndussumensis* (23.0); *C. olivaceus* (28.1); *Hemixos castanonotus* (35.0); *H. flavala* (32.5); *Hypsipetes leucocephalus* (16.0); *H. mcclellandii* (32.5); *H. thompsoni* (41.8); *Iole indica* (30.6); *I. olivacea* (25.9); *I. propinqua* (25.9); *I. virescens* (25.0); *Ixonotus guttatus* (35.2); *Ixos amaurotis* (70.9); *I. malaccensis* (37.3); *Neolestes torquatus* (22.5); *Nicator chloris* (46.2); *N. gularis* (46.5); *N. vireo* (23.6); *Phyllastrephus albigularis* (24.7); *P. baumanni* (27.6); *P. cabanisi* (25.5); *P. cerviniventis* (27.0); *P. debilis* (14.4); *P. fischeri* (27.2); *P. flavostriatus* (28.5); *P. fulviventris* (33.5); *P. hypochloris* (23.3); *P. icterinus* (19.0); *P. lorenzi* (19.0); *P. poensis* (28.9); *P. strepitans* (27.1); *P. terrestris* (29.9); *P. xavieri* (22.9); *Phylllastrephus poliocephalus* (53.0); *Pycnonotus atriceps* (25.5); *P. aurigaster* (44.4); *P. barbatus* (32.7); *P. blanfordi* (33.4); *P. brunneus* (28.8); *P. cafer* (43.0); *P. capensis* (38.6); *P. cyaniventris* (22.0); *P. erythropthalmos* (19.2); *P. eutilotus* (35.3); *P. finlaysoni* (26.3); *P. flavescens* (28.9); *P. goiavier* (27.8); *P. jocosus* (30.0); *P. leucogenys* (36.0); *P. leucotis* (27.5); *P. luteolus* (34.7); *P. melanicterus* (30.7); *P. melanoleucos* (31.0); *P. nigricans* (30.8); *P. plumosus* (34.9); *P. priocephalus* (28.7); *P. simplex* (25.1); *P. sinensis* (34.2); *P. squamatus* (22.0); *P. striatus* (52.5); *P. xantholaemus* (32.0); *P. xanthopygos* (38.1); *P. xanthorrhous*

(26.9); *P. zeylanicus* (86.5); *Pyrrhurus scandens* (43.0); *Spizixos canifrons* (44.0); *S. semitorques* (33.8); *Thescelocichla leucophleura* (62.1); *Tricholestes criniger* (17.1); *Aenigmatolimnas marginalis* (51.2); *Amaurolimnas concolor* (133.0); *Amaurornis akool* (134.0); *A. bicolor* (290.0); *A. flavirostris* (86.2); *A. olivaceus* (292.0); *A. phoenicurus* (180.0); *Anurolimnas castaneiceps* (126.0); *Aramides axillaris* (292.0); *A. cajanea* (397.0); *A. calopterus* (437.3); *A. mangle* (183.0); *A. saracura* (540.0); *A. wolfi* (454.0); *A. ypecaha* (701.0); *Carnirallus ocules* (256.9); *Coturnicops exquisitus* (24.5); *C. notatus* (30.0); *C. noveboracensis* (60.9); *Crex crex* (156.0); *C. egregia* (119.0); *Eulabeornis castaneoventris* (687.0); *Fulica americana* (642.0); *F. ardesiaca* (988.0); *F. armillata* (1040.0); *F. atra* (684.0); *F. caribaea* (345.4); *F. cornuta* (2125.0); *F. cristata* (826.0); *F. gigantea* (2455.0); *F. leucoptera* (656.0); *F. rufifrons* (644.0); *Gallicrex cinerea* (403.0); *Gallinula angulata* (132.0); *G. chloropus* (344.0); *G. tenebrosa* (532.0); *G. ventralis* (387.0); *Gallirallus philippensis* (208.0); *G. striatus* (116.0); *Laterallus albigularis* (47.4); *L. exilis* (33.6); *L. fasciatus* (66.4); *L. jamaicensis* (32.7); *L. leucopyrrhus* (45.5); *L. levraudi* (52.5); *L. melanophaius* (52.1); *L. ruber* (44.4); *L. tuerosi* (32.0); *L. viridis* (64.0); *L. xenopterus* (56.9); *Micropygia schomburgkii* (31.2); *Neocrex colombianus* (54.0); *N. erythrops* (58.3); *Pardirallus maculatus* (171.0); *P. nigricans* (217.0); *P. sanguinolentus* (232.0); *Porphyrio alleni* (140.0); *P. martinica* (236.0); *P. porphyrio* (794.0); *Porphyriops melanops* (254.9); *Porphyrula flavirostris* (92.7); *Porzana albicollis* (100.0); *P. carolina* (74.8); *P. cinerea* (52.1); *P. flaviventer* (24.9); *P. fluminea* (60.9); *P. fusca* (57.6); *P. parva* (49.7); *P. paykullii* (111.0); *P. porzana* (87.1); *P. pusilla* (35.4); *P. spiloptera* (68.5); *P. tabuensis* (42.6); *Rallina eurizonoides* (109.0); *R. fasciata* (100.0); *R. tricolor* (178.0); *Rallus aequatorialis* (89.0); *R. antarcticus* (60.4); *R. aquaticus* (112.0); *R. caerulescens* (163.0); *R. elegans* (319.0); *R. limicola* (84.1); *R. longirostris* (263.0); *R. pectoralis* (96.5); *R. semiplumbeus* (107.4); *R. wetmorei* (275.7); *Rougetius rougetii* (195.0); *Sarothrura affinis* (27.8); *S. ayresii* (31.8); *S. boehmi* (35.1); *S. elegans* (46.1); *S. lugens* (39.5); *S. pulchra* (45.2); *S. rufa* (37.7); *Andigena cucullata* (312.0); *A. hypoglauca* (314.0); *A. laminirostris* (311.0); *A. nigrirostris* (350.0); *Aulacorhynchus calorhynchus* (170.4); *A. coeruleicinctis* (208.0); *A. derbianus* (210.0); *A. haematopygus* (192.0); *A. huallagae* (269.0); *A. prasinus* (172.0); *A. sulcatus* (167.0); *Baillonius bailloni* (146.0); *Capito auratus* (62.0); *C. aurovirens* (56.2); *C. brunneipectus* (57.9); *C. dayi* (67.2); *C. hypoleucus* (58.5); *C. maculicoronatus* (47.8); *C. niger* (58.9); *C. quinticolor* (60.1); *C. squamatus* (59.5); *C. wallacei* (78.0); *Eubucco bourcierii* (37.0); *E. richardsoni* (33.9); *E. tucinkae* (41.7); *E. versicolor* (32.8); *Pteroglossus aracari* (254.0); *P. azara* (148.0); *P. beauharnaesii* (216.0); *P. bitorquatus* (142.0); *P. castanotis* (259.0); *P. erythropygius* (278.0); *P. frantzii* (253.0); *P. inscriptus* (131.0); *P. mariae* (141.0); *P. pluricinctus* (263.0); *P. sanguineus* (245.0); *P. torquatus* (197.0); *P. viridis* (135.0); *Ramphastos ambiguus* (640.0); *R. brevis* (412.0); *R. citreolaemus* (438.0); *R. dicolorus* (400.0); *R. sulfuratus* (410.0); *R. swainsonii* (678.0); *R. toco* (618.0); *R. tucanus* (595.0); *R. vitellinus* (344.0); *Selenidera culik* (147.0); *S. gouldi* (181.0); *S. maculirostris* (164.0); *S. nattereri* (159.0); *S. reinwardtii* (160.0); *S. spectabilis* (219.0); *Semnornis frantzii* (57.3); *S. ramphastinus* (97.5); *Regulus calendula* (6.2); *R. ignicapillus* (5.6); *R. regulus* (5.8); *R. satrapa* (6.2); *Rhea americana* (23000.0); *R. pennata* (23900.0); *Acropternis orthonyx* (90.0); *Eugralla paradoxa* (44.0); *Liosceles thoracicus* (40.5); *Melanopareia elegans* (16.0); *M. maranonica* (23.0); *M. maximiliani* (18.0); *M. torquata* (17.2); *Merulaxis ater* (37.2); *M. stresemanni* (84.4); *Myornis senilis* (21.2); *Psilorhamphus guttatus* (11.3); *Pteroptochos castaneus* (162.0); *P. megapodius* (114.0); *P. tarnii* (147.0); *Rhinocrypta lanceolata* (61.9); *Scelorchilus albicollis* (46.1); *S. rubecula* (76.0); *Scytalopus acutirostris* (18.1); *S. affinis* (13.2); *S. altirostris* (22.7); *S. argentifrons* (17.0); *S. atratus* (25.8); *S. bolivianus* (20.8); *S. canus* (20.3); *S. caracae* (24.0); *S. chocoensis* (20.0); *S. femoralis* (23.2); *S. fuscicauda* (12.2); *S. fuscus* (17.1); *S. griseicollis* (18.1); *S. indigoticus* (16.3); *S. iraiensis* (12.4); *S. latebricola* (21.5); *S. latrans* (17.7); *S. macropus* (37.5); *S. magellanicus* (13.7); *S. meridanus* (20.0); *S. micropterus* (29.7); *S. novacapitalis* (18.9); *S. panamensis* (21.5); *S. parkeri* (21.3); *S. parvirostris* (17.9); *S. psychopompas* (17.8); *S. robbinsi* (19.4); *S. sanctaemartae* (17.1); *S. schulenbergi* (16.1); *S. simonsi* (16.7); *S. speluncae* (13.0); *S. spillmanni* (24.7); *S. superciliaris* (17.8); *S. unicolor* (17.7); *S. urubambae* (13.0); *S. vicinior* (23.1); *S. zimmeri* (17.3); *Teledromas fuscus* (37.9); *Rhinopomastus aterrimus* (28.0); *R. cyanomelas* (28.0); *Nycticryphes semicollaris* (76.6); *Rostratula benghalensis* (121.0); *Sagittarius serpentarius* (4017.0); *Sapayoa aenigma* (20.8); *Actitis hypoleucos* (48.0); *A. macularia* (40.4); *Aphriza virgata* (201.5); *Arenaria interpres* (136.0); *A. melanocephala* (126.5); *Bartramia longicauda* (159.0); *Calidris acuminata* (66.6); *C. alba* (53.2); *C. alpina* (52.3); *C. bairdii* (41.1); *C. canutus* (142.0); *C. ferruginea* (58.1); *C. fuscicollis* (44.5); *C. himantopus* (57.4); *C. maritima* (65.2); *C. mauri* (27.9); *C. melanotos* (81.4); *C. minuta* (21.1); *C. minutilla* (22.9); *C. ptilocnemis* (86.0); *C. pusilla* (27.5); *C. ruficollis* (26.8); *C. subminuta* (30.2); *C. temminckii* (23.0); *C. tennuirostris* (192.0); *Catoptrophorus semipalmatus* (215.0); *Eury-*

norhynchus pygmaeus (31.8); *Gallinago andina* (108.0); *G. gallinago* (105.0); *G. imperialis* (190.3); *G. jamesoni* (166.0); *G. media* (170.5); *G. megala* (121.0); *G. nemoricola* (170.0); *G. nigripennis* (112.0); *G. nobilis* (192.5); *G. paraguaiae* (109.5); *G. solitaria* (140.8); *G. stenura* (113.0); *G. stricklandii* (252.0); *G. undulata* (313.0); *Heteroscelus incanus* (116.0); *Limicola falcinellus* (37.1); *Limnodromus griseus* (109.7); *L. scolopaceus* (104.5); *L. semipalmatus* (212.0); *Limosa fedoa* (358.5); *L. haemastica* (255.5); *L. lapponica* (292.5); *L. limosa* (291.0); *Lymnocryptes minimus* (50.2); *Numenius americanus* (586.5); *N. arquata* (805.5); *N. borealis* (362.0); *N. madagascariensis* (792.0); *N. minutus* (173.0); *N. phaeopus* (365.8); *N. tahitiensis* (401.0); *N. tenuirostris* (308.0); *Phalaropus fulicaria* (60.0); *P. lobatus* (36.8); *P. tricolor* (60.0); *Philomachus pugnax* (136.0); *Scolopax minor* (197.5); *S. rusticola* (308.0); *Tringa breviceps* (127.0); *T. erythropus* (158.0); *T. flavipes* (77.5); *T. glareola* (60.8); *T. melanoleuca* (162.0); *T. nebularia* (187.0); *T. ochropus* (71.4); *T. solitaria* (48.4); *T. stagnatilis* (77.5); *T. totanus* (119.0); *Tryngites subruficollis* (62.4); *Xenus cinereus* (78.8); *Scopus umbretta* (472.0); *Sitta canadensis* (9.8); *S. carolinensis* (21.0); *S. cashmirensis* (19.1); *S. castanea* (19.7); *S. europaea* (20.8); *S. frontalis* (16.5); *S. himalayensis* (14.5); *S. krüperi* (12.4); *S. leucopsis* (14.8); *S. magna* (41.5); *S. nagaensis* (14.7); *S. neumayer* (26.5); *S. pusilla* (10.2); *S. pygmaea* (10.6); *S. solangiae* (15.0); *S. tephronota* (35.2); *S. victoriae* (41.5); *S. villosa* (9.5); *S. yunnanensis* (10.3); *Tichodroma muraria* (17.6); *Steatornis caripensis* (408.0); *Aegolius acadicus* (104.0); *A. funereus* (141.0); *A. harrisii* (120.0); *A. ridgwayi* (80.0); *Asio capensis* (310.0); *A. clamator* (440.0); *A. flammeus* (378.0); *A. otus* (279.0); *A. stygius* (675.0); *Athene blewitti* (241.0); *A. brama* (112.0); *A. cunicularia* (151.0); *A. noctua* (169.0); *Bubo africanus* (645.0); *B. bengalensis* (1100.0); *B. bubo* (2686.0); *B. capensis* (1138.0); *B. coromandus* (2300.0); *B. lacteus* (2165.0); *B. leucostictus* (533.0); *B. magellanicus* (1171.0); *B. nipalensis* (1400.0); *B. poensis* (661.0); *B. shelleyi* (1257.0); *B. sumatranus* (1525.0); *B. virginianus* (1192.0); *Glaucidium albertinum* (73.0); *G. bolivianum* (63.1); *G. brasilianum* (70.8); *G. brodiei* (59.5); *G. capense* (122.0); *G. costaricanum* (199.0); *G. cuculoides* (163.0); *G. gnoma* (61.6); *G. griseiceps* (50.6); *G. hardyi* (58.3); *G. hoskinsii* (57.5); *G. jardinii* (66.9); *G. minutissimum* (50.0); *G. nanum* (74.1); *G. nubicola* (77.6); *G. palmarum* (45.7); *G. parkeri* (61.4); *G. passerinum* (54.8); *G. perlatum* (80.0); *G. peruanum* (62.5); *G. radiatum* (101.0); *G. sanchezi* (55.0); *G. sjostedti* (139.0); *G. tephronotum* (87.4); *Jubula lettii* (183.0); *Ketupa blakistoni* (3750.0); *K. flavipes* (2315.0); *K. ketupu* (1293.0); *K. zeylonensis* (1105.0); *Lophostrix cristata* (544.0); *Micrathene whitneyi* (41.0); *Ninox connivens* (557.0); *N. novaeseelandiae* (181.0); *N. rufa* (954.0); *N. scutulata* (191.0); *N. strenua* (1350.0); *Nyctea scandiaca* (1963.0); *Otus albogularis* (185.0); *O. asio* (194.0); *O. atricapillus* (190.0); *O. bakkamoena* (114.0); *O. barbarus* (69.0); *O. brucei* (86.8); *O. centralis* (145.5); *O. choliba* (147.0); *O. clarkii* (186.0); *O. cooperi* (170.0); *O. flammeolus* (60.2); *O. guatemalae* (150.0); *O. hoyi* (145.0); *O. icterorhynchus* (73.3); *O. ingens* (175.0); *O. ireneae* (50.3); *O. kennicottii* (186.0); *O. koepckeae* (121.0); *O. leucotis* (200.0); *O. marshalli* (115.0); *O. petersoni* (97.5); *O. roboratus* (162.0); *O. roraimae* (105.0); *O. rufescens* (76.8); *O. sagittatus* (124.0); *O. sanctaecatarinae* (211.0); *O. scops* (92.0); *O. seductus* (160.0); *O. senegalusis* (71.0); *O. spilocephalus* (67.5); *O. sunia* (77.0); *O. trichopsis* (92.2); *O. watsonii* (130.0); *Pulsatrix koeniswaldiana* (48.0); *P. melanota* (699.9); *P. perspicillata* (1001.0); *Scotopelia bouvieri* (637.0); *S. peli* (1957.0); *S. ussheri* (789.0); *Strix albitarsis* (353.9); *S. aluco* (475.0); *S. butleri* (219.0); *S. chacoensis* (330.0); *S. davidi* (785.0); *S. fulvescens* (557.1); *S. huhula* (385.0); *S. hylophila* (395.0); *S. leptogrammica* (1023.0); *S. nebulosa* (1079.0); *S. nigrolineata* (375.0); *S. occidentalis* (588.0); *S. ocellata* (653.3); *S. rufipes* (380.0); *S. uralensis* (785.0); *S. varia* (717.0); *S. virgata* (260.0); *S. woodfordii* (350.0); *Surnia ulula* (321.0); *Xenoglaux loweryi* (48.0); *Struthio camelus* (111000.0); *Acridotheres albocinctus* (77.4); *A. cinereus* (113.0); *A. cristatellus* (117.0); *A. fuscus* (82.8); *A. ginginianus* (72.0); *A. grandis* (99.0); *A. tristis* (113.0); *Ampeliceps coronatus* (88.5); *Aplonis metallica* (56.5); *A. panayensis* (56.2); *Buphagus africanus* (60.3); *B. erythrorhynchus* (50.8); *Cinnyricinclus leucogaster* (44.0); *Creatophora cinerea* (73.1); *Dumetella carolinensis* (35.3); *D. glabrirostris* (36.3); *Gracula religiosa* (192.0); *Gracupica nigricollis* (157.0); *Grafisia torquata* (64.0); *Lamprotornis acuticaudus* (67.6); *L. australis* (106.0); *L. caudatus* (121.0); *L. chalcurus* (63.0); *L. chalybaeus* (86.5); *L. chloropterus* (73.1); *L. corruscus* (56.8); *L. cupreocauda* (58.5); *L. fischeri* (48.5); *L. hildebrandti* (55.9); *L. iris* (49.0); *L. mevesii* (64.2); *L. nitens* (85.6); *L. pulcher* (67.3); *L. purpureiceps* (64.5); *L. purpureus* (116.0); *L. purpuropterus* (78.5); *L. regius* (54.5); *L. shelleyi* (45.0); *L. splendidus* (125.0); *L. superbus* (64.9); *L. unicolor* (60.5); *Melanotis caerulescens* (61.6); *M. hypoleucus* (68.0); *Mimus dorsalis* (58.7); *M. gilvus* (52.4); *M. longicaudatus* (66.6); *M. patagonicus* (57.8); *M. polyglottos* (48.5); *M. saturninus* (63.7); *M. thenca* (66.0); *M. triurus* (47.2); *Neocichla gutturalis* (66.7); *Onychognathus alvirostris* (138.0); *O. blythii* (100.0); *O. fulgidus* (112.0); *O. morio* (137.5); *O. nabouroup* (104.0); *O. neumanni* (105.0); *O. salvadorii*

(148.0); *O. tenuirostris* (126.0); *O. tristramii* (123.0); *O. walleri* (87.8); *Oreoscoptes montanus* (44.2); *Pholia femoralis* (46.0); *P. sharpii* (44.5); *Poeoptera kenricki* (46.8); *P. lugubris* (39.0); *P. stuhlmanni* (39.5); *Saroglossa spiloptera* (47.5); *Speculipastor bicolor* (64.3); *Spreo albicapillus* (113.0); *S. bicolor* (104.0); *Sturnia sturninus* (61.0); *Sturnus burmannicus* (89.0); *S. cineraceus* (83.0); *S. contra* (84.0); *S. malabaricus* (36.4); *S. nigricollis* (131.0); *S. pagodarum* (74.0); *S. roseus* (74.0); *S. sericeus* (76.0); *S. sinensis* (61.0); *S. unicolor* (85.0); *S. vulgaris* (74.1); *Toxostoma bendirei* (62.2); *T. cinereum* (59.2); *T. crissale* (62.7); *T. curvirostre* (81.8); *T. lecontei* (61.9); *T. longirostre* (67.6); *T. ocellatum* (84.3); *T. redivivum* (84.4); *T. rufum* (68.8); *Abroscopus albogularis* (5.0); *A. schisticeps* (4.7); *A. superciliaris* (6.5); *Acrocephalus aedon* (22.4); *A. agricola* (9.6); *A. arundinaceus* (30.0); *A. baeticatus* (10.2); *A. bistrigiceps* (8.7); *A. concinens* (8.3); *A. dumetorum* (11.2); *A. gracilirostris* (14.4); *A. melanopogon* (10.9); *A. orientalis* (25.5); *A. paludicola* (11.6); *A. palustris* (11.5); *A. rufescens* (22.8); *A. schoenobaenus* (11.9); *A. scirpaceus* (12.3); *A. sorghophilus* (10.5); *A. stentoreus* (24.2); *A. tangorum* (16.4); *Actinodura egertoni* (36.0); *A. nipalensis* (44.0); *A. ramsayi* (38.4); *A. souliei* (45.0); *A. waldeni* (47.5); *Alcippe brunnea* (17.5); *A. brunneicauda* (14.3); *A. castaneceps* (12.5); *A. chrysotis* (10.0); *A. cinerea* (11.0); *A. cinereiceps* (10.0); *A. dubia* (16.0); *A. ludlowi* (11.0); *A. morrisonia* (15.5); *A. nipalensis* (15.8); *A. peracensis* (15.0); *A. poiocephala* (20.7); *A. ruficapilla* (12.0); *A. rufogularis* (15.8); *A. striaticollis* (17.0); *A. variegaticeps* (13.0); *A. vinipectus* (12.0); *Babax koslowi* (90.0); *B. lanceolatus* (90.0); *B. waddelli* (110.0); *Bathmocercus cerviniventris* (15.8); *B. rufus* (15.5); *B. winifredae* (15.5); *Bradypterus alfredi* (17.5); *B. baboecala* (12.9); *B. barratti* (18.8); *B. carpalis* (22.4); *B. cinnamomeus* (17.4); *B. grandis* (18.5); *B. graueri* (17.0); *B. lopezi* (20.0); *B. luteoventris* (13.2); *B. major* (10.8); *B. seebohmi* (11.3); *B. sylvaticus* (17.0); *B. tacsanowskius* (14.0); *B. thoracicus* (10.8); *B. victorini* (10.0); *Cettia acanthizoides* (5.5); *C. brunnifrons* (7.5); *C. canturians* (10.0); *C. cetti* (13.4); *C. diphone* (13.5); *C. flavolivacea* (8.0); *C. fortipes* (9.8); *C. major* (13.0); *C. pallidipes* (7.7); *Chaetornis striatus* (35.0); *Chamaea fasciata* (15.0); *Chloropeta natalensis* (11.7); *C. similis* (11.1); *Chrysomma altirostris* (16.0); *C. poecilotis* (14.0); *C. sinense* (17.2); *Cichlopsis leucogenys* (54.2); *Cincloramphus cruralis* (53.6); *C. mathewsi* (30.3); *Conostoma oemodium* (84.0); *Crocias langbianis* (45.0); *Cutia nipalensis* (49.5); *Dumetia hyperythra* (12.9); *Entomodestes coracinus* (56.0); *E. leucotis* (61.7); *Eremiornis carteri* (12.2); *Eremomela atricollis* (10.2); *E. badiceps* (10.6); *E. canescens* (7.0); *E. flavicrissalis* (4.5); *E. gregalis* (6.8); *E. icteropygialis* (7.6); *E. pusilla* (6.2); *E. salvadorii* (8.0); *E. scotops* (9.0); *E. turneri* (7.5); *E. usticollis* (8.4); *Gampsorhynchus rufulus* (37.0); *Garrulax affinis* (73.0); *G. albogularis* (98.5); *G. austeni* (63.8); *G. bieti* (75.0); *G. cachinnans* (43.0); *G. caerulatus* (86.0); *G. canorus* (63.0); *G. chinensis* (110.0); *G. cineraceus* (49.0); *G. davidi* (56.2); *G. delesserti* (92.0); *G. elliotii* (45.0); *G. erythrocephalus* (71.7); *G. formosus* (110.0); *G. galbanus* (56.0); *G. gularis* (92.0); *G. henrici* (78.0); *G. jerdoni* (45.5); *G. leucolophus* (124.0); *G. lineatus* (40.7); *G. lugubris* (82.0); *G. lunulatus* (70.0); *G. maesi* (105.0); *G. maximus* (120.0); *G. merulinus* (78.8); *G. milleti* (105.0); *G. milnei* (100.0); *G. mitratus* (62.0); *G. monileger* (84.0); *G. nuchalis* (78.0); *G. ocellatus* (114.0); *G. pectoralis* (146.0); *G. perspicillatus* (118.0); *G. poecilorhynchus* (72.0); *G. ruficollis* (66.5); *G. rufogularis* (63.0); *G. sannio* (67.8); *G. squamatus* (84.0); *G. strepitans* (105.0); *G. striatus* (117.0); *G. subunicolor* (66.0); *G. sukatschewi* (67.8); *G. variegatus* (64.5); *G. vassali* (110.0); *G. virgatus* (48.0); *G. yersini* (110.0); *Graminicola bengalensis* (14.8); *Graueria vittata* (15.6); *Hemitesia neumanni* (14.2); *Heterophasia annectens* (24.5); *H. capistrata* (39.4); *H. gracilis* (38.0); *H. melanoleuca* (32.6); *H. picaoides* (42.4); *H. pulchella* (41.0); *Hippolais caligata* (8.9); *H. icterina* (13.2); *H. languida* (12.0); *H. olivetorum* (17.5); *H. pallida* (9.0); *H. polyglotta* (11.0); *Hylia prasina* (13.1); *Hyliota australis* (11.2); *H. flavigaster* (12.5); *H. usambarae* (10.1); *H. violacea* (15.8); *Hylocichla mustelina* (50.2); *Illadopis albipectus* (30.6); *I. cleaveri* (30.8); *I. fulvescens* (27.9); *I. puveli* (48.4); *I. pyrrhoptera* (18.8); *I. rufescens* (37.0); *I. rufipennis* (22.2); *Ixoreus naevius* (77.6); *Jabouilleia danjoui* (30.0); *Kakamega poliothorax* (36.4); *Kenopia striata* (19.9); *Kupeornis chapini* (8.8); *K. gilberti* (28.7); *K. rufocinctus* (47.0); *Leiothrix argentauris* (28.4); *L. lutea* (21.4); *Leptopoecile elegans* (6.3); *L. sophiae* (6.9); *Liocichla omeiensis* (44.0); *L. phoenicea* (49.0); *Lioptilus nigricapillus* (29.7); *Locustella certhiola* (14.4); *L. fasciolata* (27.2); *L. fluviatilis* (16.1); *L. lanceolata* (10.6); *L. lusciniodes* (13.9); *L. naevia* (13.3); *L. ochotensis* (18.5); *L. pleskei* (15.3); *L. pryeri* (16.3); *Macronous gularis* (12.0); *M. kelleyi* (16.0); *M. ptilosus* (18.0); *Macrosphenus concolor* (13.9); *M. flavicans* (13.4); *M. kempi* (12.7); *M. kretschmeri* (20.0); *M. pulitzeri* (15.0); *Malacocincla abbotti* (29.5); *Malacopteron affine* (17.2); *M. cinereum* (18.1); *M. magnirostre* (19.4); *M. magnum* (27.2); *Megalurus gramineus* (14.1); *M. palustris* (44.9); *M. timoriensis* (18.1); *Melocichla mentalis* (33.2); *Minla cyanouroptera* (17.0); *M. ignotincta* (14.3); *M. strigula* (19.2); *Myadestes coloratus* (29.1); *M. melanops* (32.1); *M. occidentalis* (36.4); *M. ralloides* (29.1); *M. townsendi* (33.2); *M. unicolor* (37.9); *Myzornis pyr-*

rhoura (11.9); *Napothera brevicaudata* (19.5); *N. crispifrons* (27.0); *N. epilepidota* (16.0); *N. macrodactyla* (48.7); *N. marmorata* (32.2); *Orthotomus atrogularis* (7.7); *O. cuculatus* (5.9); *O. ruficeps* (6.5); *O. sericeus* (10.8); *O. sutorius* (7.5); *Panurus biarmicus* (13.9); *Paradoxornis alphonsianus* (14.7); *P. atrosuperciliaris* (16.8); *P. brunneus* (6.0); *P. conspicillatus* (14.0); *P. davidianus* (5.0); *P. flavirostris* (26.0); *P. fulvifrons* (6.4); *P. gularis* (29.0); *P. guttaticollis* (26.0); *P. heudei* (29.0); *P. nipalensis* (5.5); *P. paradoxus* (37.0); *P. przewalskii* (13.0); *P. ruficeps* (32.0); *P. unicolor* (34.0); *P. verreauxi* (6.0); *P. webbianus* (10.9); *P. zappeyi* (10.0); *Parisoma boehmi* (14.0); *P. Buryi* (14.5); *P. layardi* (14.5); *P. lugens* (15.0); *P. subcaeruleum* (14.3); *Parophasma galinieri* (21.5); *Pellorneum albiventre* (21.5); *P. capistratum* (25.1); *P. palustre* (18.0); *P. ruficeps* (26.0); *P. tickelli* (17.1); *Phyllanthus atripennis* (85.8); *Phyllolais pulchella* (6.0); *Phylloscopus affinis* (7.0); *P. armandii* (9.4); *P. bonelli* (8.7); *P. borealis* (10.9); *P. budongoenis* (8.2); *P. cantator* (6.0); *P. chloronotus* (5.1); *P. collybita* (8.3); *P. coronatus* (10.1); *P. davisoni* (6.4); *P. emeiensis* (8.2); *P. fuligiventer* (9.3); *P. fuscatus* (8.8); *P. griseolus* (7.6); *P. herberti* (8.9); *P. humei* (6.0); *P. inornatus* (6.6); *P. kansuensis* (6.3); *P. laetus* (9.6); *P. laurae* (8.5); *P. maculipennis* (5.1); *P. magnirostris* (11.6); *P. neglectus* (5.3); *P. occipitalis* (9.0); *P. plumbeitarsus* (8.0); *P. proregulus* (6.0); *P. pulcher* (6.8); *P. reguloides* (7.8); *P. ricketti* (7.4); *P. ruficapilla* (7.7); *P. schwarzi* (11.5); *P. sibilatrix* (9.2); *P. sichuanensis* (3.5); *P. sindhianus* (7.6); *P. subaffinis* (6.2); *P. subviridis* (5.5); *P. tenellipes* (11.8); *P. trivirgatus* (9.0); *P. trochiloides* (8.0); *P. trochilus* (8.7); *P. tytleri* (7.2); *P. umbrovirens* (8.6); *Platycichla flavipes* (64.0); *P. leucops* (62.4); *Pnoepyga albiventer* (20.9); *P. immaculata* (20.5); *P. pusilla* (12.0); *Poliolais lopesi* (12.0); *Pomatorhinus erythrocnemis* (58.8); *P. erythrogenys* (54.9); *P. ferruginosus* (40.0); *P. horsfieldii* (43.0); *P. hypoleucos* (75.6); *P. montanus* (28.7); *P. ochraceiceps* (34.0); *P. ruficollis* (31.7); *P. schisticeps* (43.0); *Pseudoalcippe abyssinica* (5.5); *Pteruthius aenobarbus* (13.3); *P. flaviscapis* (39.0); *P. melanotis* (13.3); *P. rufiventer* (44.5); *P. xanthochlorus* (14.3); *Ptyrticus turdinus* (65.8); *Rhopocichla atriceps* (16.3); *Ridgwayia pinicola* (88.0); *Rimator malacoptilus* (19.5); *Schistolais leucopogon* (12.2); *Schoenicola platyura* (15.5); *Seicercus affinis* (7.0); *S. burkii* (7.3); *S. castaniceps* (5.3); *S. montis* (6.4); *S. poliogenys* (6.3); *S. xanthoschistos* (7.1); *Sialia currucoides* (29.6); *S. mexicana* (26.5); *S. sialis* (27.5); *Spelaeornis badeigularis* (11.0); *S. caudatus* (11.0); *S. chocolatinus* (12.0); *S. formosus* (12.0); *S. longicaudatus* (12.0); *S. troglodytoides* (12.0); *Sphenocichla humei* (34.1); *Sphenoeacus afer* (30.4); *Stachyris ambigua* (9.7); *S. chrysaea* (9.0); *S. herberti* (29.0); *S. leucotis* (23.7); *S. maculata* (29.2); *S. nigriceps* (15.8); *S. nigricollis* (26.2); *S. oglei* (33.0); *S. poliocephala* (23.4); *S. pyrrhops* (9.8); *S. rodolphei* (12.0); *S. ruficeps* (10.3); *S. rufifrons* (10.6); *S. striolata* (29.0); *Sylvia atrcapilla* (16.7); *S. borin* (18.2); *S. cantillans* (9.6); *S. communis* (15.1); *S. conspicillata* (9.0); *S. curruca* (11.1); *S. curruca althaea* (11.8); *S. deserticola* (8.6); *S. hortensis* (21.9); *S. leucomelaena* (13.9); *S. melanocephala* (11.7); *S. minula* (10.0); *S. mystacea* (9.9); *S. nana* (8.7); *S. nisoria* (22.5); *S. rueppeli* (12.9); *S. undata* (10.8); *Sylvietta brachyura* (8.1); *S. denti* (8.4); *S. isabellina* (10.0); *S. leucophrys* (11.4); *S. philippae* (8.6); *S. rufescens* (11.6); *S. ruficapilla* (11.1); *S. virens* (8.4); *S. whytii* (9.9); *Tesia castaneocoronata* (9.0); *T. cyaniventer* (9.7); *T. olivea* (7.0); *Tickellia hodgsoni* (4.5); *Timalia pileata* (16.0); *Trichastoma bicolor* (27.2); *T. rostratum* (22.7); *Turdoides affinis* (37.0); *T. altirostris* (33.0); *T. aylmeri* (35.3); *T. bicolor* (78.3); *T. caudatus* (39.7); *T. earlei* (47.0); *T. gularis* (45.5); *T. gymnogenys* (77.0); *T. hartlaubii* (86.2); *T. hindei* (67.6); *T. hypoleucus* (74.0); *T. jardineii* (78.2); *T. leucocephalus* (64.0); *T. leucopygius* (82.4); *T. longirostris* (35.0); *T. malcolmi* (75.7); *T. melanops* (77.0); *T. nipalensis* (68.0); *T. plebejus* (62.5); *T. reinwardtii* (78.8); *T. rubiginosus* (40.6); *T. sharpei* (79.3); *T. squamiceps* (73.5); *T. squamulatus* (69.0); *T. striatus* (69.5); *T. subrufus* (67.5); *T. tenebrosus* (76.0); *Urorhipis rufifrons* (6.7); *Urosphena squameiceps* (9.3); *Xiphirhynchus superciliaris* (28.0); *Yuhina bakeri* (17.5); *Y. castaniceps* (11.8); *Y. diademata* (12.0); *Y. flavicollis* (17.5); *Y. gularis* (21.0); *Y. humilis* (12.0); *Y. nigrimenta* (9.5); *Y. occipitalis* (13.0); *Y. zantholeuca* (11.8); *Batara cinerea* (131.0); *Biatas nigropectus* (34.2); *Cercomacra brasiliana* (15.9); *C. carbonaria* (14.5); *C. cinerascens* (14.3); *C. ferdinandi* (15.0); *C. laeta* (16.0); *C. manu* (18.2); *C. melanaria* (19.0); *C. nigrescens* (16.5); *C. nigricans* (16.6); *C. parkeri* (17.3); *C. serva* (17.0); *C. tyrannina* (16.3); *Clytoctantes alixii* (31.2); *C. atrogularis* (31.0); *Cymbilaimus lineatus* (35.8); *C. sanctaemariae* (28.7); *Dichrozona cincta* (16.0); *Drymophila caudata* (11.9); *D. devillei* (10.2); *D. ferruginea* (10.6); *D. genei* (19.3); *D. malura* (13.0); *D. ochropyga* (10.5); *D. rubricollis* (10.0); *D. squamata* (10.8); *Dysithamnus leucostictus* (20.2); *D. mentalis* (16.3); *D. occidentalis* (19.3); *D. plumbeus* (20.5); *D. puncticeps* (14.9); *D. stictothorax* (12.9); *D. striaticeps* (12.0); *D. tucuyensis* (20.0); *D. xanthopterus* (15.1); *Formicivora acutirostris* (19.3); *F. erythronotos* (7.9); *F. grisea* (10.4); *F. iheringi* (8.2); *F. intermedia* (9.4); *F. littoralis* (15.0); *F. melanogaster* (10.5); *F. rufa* (10.8); *F. serrana* (12.0); *Frederickena unduligera* (83.0); *F. viridis* (76.0); *Gymnocichla nudiceps* (30.5); *Gymnopithys leucaspis* (31.1); *G. lunulata* (24.0); *G. rufigula*

(29.1); *G. salvini* (25.9); *Herpsilochmus atricapillus* (10.8); *H. axillaris* (11.4); *H. dorsimaculatus* (9.9); *H. dugandi* (10.3); *H. gentryi* (10.6); *H. longirostris* (12.8); *H. motacilloides* (12.5); *H. parkeri* (10.0); *H. pectoralis* (10.0); *H. pileatus* (8.9); *H. roraimae* (11.8); *H. rufimarginatus* (10.6); *H. sellowi* (7.5); *H. stictocephalus* (8.8); *H. sticturus* (9.5); *Hylophylax naevia* (14.2); *H. naevioides* (17.8); *H. poecilinota* (18.4); *H. punctulata* (12.4); *Hypocnemis cantator* (12.6); *H. hypoxantha* (11.7); *Hypocnemoides maculicauda* (11.8); *H. melanopogon* (14.1); *Hypoedaleus guttatus* (38.8); *Mackenziaena leachii* (70.2); *M. severa* (51.8); *Megastictus margaritatus* (20.2); *Microrhopias quixensis* (7.9); *Myrmeciza atrothorax* (16.1); *M. berlepschi* (17.8); *M. disjuncta* (15.0); *M. exsul* (26.5); *M. ferruginea* (26.1); *M. fortis* (46.5); *M. goeldii* (42.0); *M. griseiceps* (15.0); *M. hemimelaena* (16.0); *M. hyperythra* (41.0); *M. immaculata* (47.1); *M. laemosticta* (25.0); *M. longipes* (27.9); *M. loricata* (29.1); *M. melanoceps* (38.5); *M. nigricauda* (24.0); *M. pelzelni* (17.8); *M. ruficauda* (24.9); *M. squamosa* (18.5); *Myrmoborus leucophrys* (21.5); *M. lugubris* (21.5); *M. melanurus* (15.1); *M. myotherinus* (18.8); *Myrmochanes hemileucus* (12.5); *Myrmorchilus strigilatus* (23.0); *Myrmornis torquata* (46.7); *Myrmotherula ambigua* (6.7); *M. assimilis* (9.3); *M. axillaris* (8.4); *M. behni* (8.0); *M. brachyura* (6.4); *M. cherriei* (8.2); *M. erythrura* (11.4); *M. fjeldsaai* (9.8); *M. fluminensis* (9.0); *M. fulviventris* (10.4); *M. grisea* (8.4); *M. gularis* (11.3); *M. guttata* (11.0); *M. gutturalis* (9.2); *M. haematonota* (8.7); *M. hauxwelli* (10.7); *M. ignota* (7.1); *M. iheringi* (8.0); *M. klagesi* (7.8); *M. leucophthalma* (9.4); *M. longicauda* (8.3); *M. longipennis* (9.4); *M. luctuosa* (8.7); *M. menetriesii* (8.6); *M. minor* (6.4); *M. multostriata* (8.0); *M. obscura* (7.1); *M. ornata* (9.4); *M. pacifica* (10.1); *M. schisticolor* (9.6); *M. sclateri* (8.4); *M. snowi* (8.4); *M. spodionota* (10.7); *M. sunensis* (8.4); *M. surinamensis* (8.3); *M. unicolor* (11.5); *M. urosticta* (11.1); *Neoctantes niger* (32.0); *Percnostola lophotes* (28.0); *P. minor* (24.8); *P. rufifrons* (24.0); *Phaenostictus mcleannani* (51.1); *Phlegopsis erythroptera* (51.1); *P. nigromaculata* (44.5); *Pithys albifrons* (20.4); *P. castanea* (29.8); *Pygiptila stellaris* (24.1); *Pyriglena atra* (32.0); *P. leuconota* (32.3); *P. leucoptera* (28.8); *Rhegmatorhina berlepschi* (23.6); *R. cristata* (25.7); *R. gymnops* (28.5); *R. hoffmannsi* (31.4); *R. melanosticta* (30.6); *Rhopornis ardesiaca* (26.3); *Sakesphorus bernardi* (34.4); *S. canadensis* (24.4); *S. cristatus* (17.7); *S. luctuosus* (31.4); *S. melanonotus* (31.8); *S. melanothorax* (31.0); *Schistocichla caurensis* (39.0); *S. leucostigma* (24.0); *S. schistacea* (20.6); *Sclateria naevia* (24.6); *Skutchia borbae* (50.0); *Taraba major* (59.2); *Terenura callinota* (7.0); *T. humeralis* (7.3); *T. maculata* (6.5); *T. sharpei* (7.5); *T. sicki* (6.4); *T. spodioptila* (6.5); *Thamnistes anabatinus* (20.7); *Thamnomanes ardesiacus* (17.7); *T. caesius* (15.7); *T. saturninus* (20.4); *T. schistogynus* (17.2); *Thamnophilus aethiops* (25.7); *T. amazonicus* (19.4); *T. ambiguus* (23.6); *T. aroyae* (20.0); *T. atrinucha* (23.6); *T. bridgesi* (27.0); *T. caerulescens* (21.1); *T. cryptoleucus* (27.5); *T. doliatus* (27.9); *T. insignis* (24.9); *T. leucogaster* (21.8); *T. multistriatus* (27.5); *T. murinus* (19.3); *T. nigriceps* (22.9); *T. nigrocinereus* (30.0); *T. palliatus* (23.3); *T. pelzelni* (20.9); *T. praecox* (23.0); *T. punctatus* (19.4); *T. ruficapillus* (20.4); *T. schistaceus* (20.3); *T. stictocephalus* (21.5); *T. sticturus* (18.2); *T. tenuepunctatus* (22.5); *T. torquatus* (21.1); *T. unicolor* (24.2); *T. zarumae* (22.8); *Xenornis setifrons* (24.6); *Attagis gayi* (311.0); *A. malouinus* (340.0); *Thinocorus orbignyianus* (115.0); *T. rumicivorus* (53.1); *Ajaia ajaja* (1496.0); *Bostrychia carunculata* (1360.9); *B. hagedash* (1238.0); *B. olivaecea* (1360.9); *B. rara* (1237.4); *Cercibis oxycerca* (1373.5); *Eudocimus albus* (900.0); *E. ruber* (665.0); *Geronticus calvus* (1630.0); *G. eremita* (1202.0); *Harpiprion caerulescens* (878.6); *Mesembrinibis cayennensis* (756.0); *Nipponia nippon* (1900.0); *Phimosus infuscatus* (559.0); *Platalea alba* (1521.0); *P. leucorodia* (1868.0); *Platelea flavipes* (1748.0); *P. regia* (1731.0); *Plegadis chihi* (622.0); *P. falcinellus* (634.0); *P. ridgwayi* (584.0); *Pseudibis davisoni* (1588.0); *P. gigantea* (3515.0); *P. papillosa* (1350.0); *Theristicus caudatus* (1726.0); *T. melanopis* (1600.0); *Threskiornis aethiopica* (1498.0); *T. melanocephalus* (1573.0); *T. spinicollis* (1352.0); *Crypturellus atrocapillus* (453.0); *C. bartletti* (241.0); *C. berlepschi* (521.0); *C. boucardi* (436.0); *C. brevirostris* (294.6); *C. casiquiare* (316.8); *C. cinereus* (509.0); *C. cinnamomeus* (422.0); *C. duidae* (426.0); *C. erythropus* (485.0); *C. kerriae* (294.6); *C. noctivagus* (562.0); *C. obsoletus* (444.0); *C. parvirostris* (200.0); *C. ptaritepui* (486.0); *C. saltuarius* (486.0); *C. soui* (217.0); *C. strigulosus* (431.0); *C. tataupa* (220.0); *C. transfasciatus* (283.0); *C. undulatus* (567.0); *C. variegatus* (378.0); *Eudromia elegans* (704.0); *E. formosa* (1070.0); *Nothocercus bonapartei* (763.0); *N. julius* (1070.0); *N. nigrocapillus* (721.8); *Nothoprocta cinerascens* (663.8); *N. curvirostris* (376.0); *N. kalinowskii* (779.8); *N. ornata* (622.0); *N. pentlandii* (303.0); *N. perdicaria* (458.0); *N. taczanowskii* (458.0); *Nothura boraquira* (283.0); *N. chacoensis* (210.0); *N. darwinii* (246.0); *N. maculosa* (259.0); *N. minor* (166.0); *Rhynchotus maculicollis* (1070.0); *R. rufescens* (845.0); *Taoniscus nanus* (43.0); *Tinamotis ingoufi* (837.9); *T. pentlandii* (650.0); *Tinamus guttatus* (688.0); *T. major* (894.0); *T. osgoodi* (1285.0); *T. solitarius* (1550.0); *T. tao* (2000.0); *Abeillia abeillei* (2.7); *Adelomyia melanogenys* (5.0); *Aglaeactis aliciae* (6.6); *A. castelnaudii* (6.7); *A.*

cupripennis (7.6); *A. pamela* (5.5); *Aglaiocercus berlepschi* (5.0); *A. coelestis* (5.7); *A. kingi* (4.9); *Amazilia amabilis* (4.2); *A. amazilia* (4.3); *A. beryllina* (4.4); *A. boucardi* (4.5); *A. brevirostris* (4.3); *A. candida* (3.8); *A. castaneiventris* (5.0); *A. cupreicauda* (3.8); *A. cyanifrons* (5.0); *A. cyanocephala* (5.1); *A. cyanura* (4.5); *A. decora* (4.5); *A. edward* (4.6); *A. fimbriata* (5.0); *A. franciae* (5.0); *A. lactea* (4.3); *A. leucogaster* (4.7); *A. luciae* (4.6); *A. rosenbergi* (4.5); *A. rutila* (5.3); *A. saucerrottei* (4.5); *A. tobaci* (4.7); *A. tzacatl* (4.8); *A. versicolor* (4.1); *A. violiceps* (5.1); *A. viridifrons* (6.3); *A. viridigaster* (3.8); *A. wagneri* (5.1); *A. yucatanensis* (3.9); *Androdon aequatorialis* (7.3); *Anopetia gounellei* (5.4); *Anthocephala floriceps* (3.6); *Anthracothorax nigricollis* (7.0); *A. prevostii* (6.4); *A. veraguensis* (7.5); *A. viridigula* (7.5); *Aphantochroa cirrochloris* (7.3); *Archilochus alexandri* (3.4); *A. colubris* (3.1); *Atthis ellioti* (2.9); *A. heloisa* (2.2); *Augastes lumachellus* (4.0); *A. scutatus* (3.0); *Avocettula recurvirostris* (4.2); *Basilinna leucotis* (4.0); *B. xantusii* (3.9); *Boissonneaua flavescens* (8.2); *B. jardini* (9.1); *B. matthewsii* (7.7); *Calliphlox amethystina* (2.8); *C. bryantae* (3.3); *C. mitchellii* (3.1); *Calothorax eliza* (4.7); *C. enicura* (5.9); *C. lucifer* (3.3); *C. pulcher* (2.7); *Calypte anna* (4.3); *C. costae* (3.1); *Campylopterus curvipennis* (6.0); *C. cuvierii* (8.8); *C. duidae* (6.1); *C. ensipennis* (9.6); *C. excellens* (8.8); *C. falcatus* (7.2); *C. hemileucurus* (9.8); *C. hyperythrus* (6.4); *C. largipennis* (8.3); *C. phainopeplus* (8.6); *C. rufus* (7.2); *C. villaviscensio* (7.5); *Chaetocercus astreans* (2.6); *C. berlepschi* (3.0); *C. bombus* (6.5); *C. heliodor* (2.8); *C. jourdanii* (7.0); *C. mulsant* (3.9); *Chalcostigma herrani* (5.8); *C. heteropogon* (5.0); *C. olivaceum* (5.6); *C. ruficeps* (3.4); *C. stanleyi* (5.8); *Chalybura buffonii* (6.8); *C. urochrysia* (6.4); *Chlorestes notatus* (3.8); *Chlorostilbon alice* (3.6); *C. assimilis* (3.0); *C. aureoventris* (3.5); *C. auriceps* (2.2); *C. canivetii* (2.5); *C. gibsoni* (2.8); *C. melanorhynchus* (2.8); *C. mellisugus* (2.7); *C. olivaresi* (3.7); *C. poortmani* (3.6); *C. russatus* (3.4); *C. stenurus* (3.3); *Chrysolampis mosquitus* (3.9); *Chrysuronia oenone* (5.1); *Clytolaema rubricauda* (7.9); *Coeligena bonapartei* (6.5); *C. coeligena* (6.8); *C. eos* (6.6); *C. helianthea* (6.7); *C. inca* (7.1); *C. iris* (6.9); *C. lutetiae* (7.3); *C. phalerata* (6.1); *C. prunellei* (7.0); *C. torquata* (6.8); *C. violifer* (7.4); *C. wilsoni* (6.7); *Colibri coruscans* (6.7); *C. delphinae* (6.4); *C. serrirostris* (6.7); *C. thalassinus* (5.9); *Cynanthus doubledayi* (3.9); *C. latirostris* (3.1); *C. sordidus* (4.0); *Damophila julie* (3.3); *Discosura conversii* (3.0); *D. langsdorffi* (3.4); *D. longicauda* (3.4); *D. popelairii* (2.2); *Doryfera johannae* (5.0); *D. ludovicae* (6.0); *Elvira chionura* (3.0); *E. cupreiceps* (3.0); *Ensifera ensifera* (11.2); *Eriocnemis alinae* (4.3); *E. cupreoventris* (5.3); *E. derbyi* (4.8); *E. glaucopoides* (3.7); *E. godini* (4.8); *E. luciani* (6.0); *E. mirabilis* (3.7); *E. mosquera* (5.3); *E. nigrivestis* (4.2); *E. sapphiropygia* (6.0); *E. vestitus* (4.6); *Eugenes fulgens* (8.2); *Eulidia yarrellii* (2.8); *Eupetomena macroura* (9.0); *Eupherusa cyanophrys* (4.8); *E. eximia* (4.3); *E. nigriventris* (3.4); *E. poliocerca* (4.9); *Eutoxeres aquila* (10.6); *E. condamini* (10.9); *Florisuga fuscus* (8.1); *F. mellivora* (7.4); *Glaucis aenea* (4.8); *G. dohrnii* (5.8); *G. hirsuta* (6.7); *Goethalsia bella* (3.4); *Goldmania violiceps* (4.1); *Haplophaedia aureliae* (5.2); *H. lugens* (6.9); *Heliactin bilopha* (4.4); *Heliangelus amethysticollis* (5.1); *H. clarisse* (5.3); *H. exortis* (4.6); *H. mavors* (4.2); *H. micraster* (4.0); *H. regalis* (3.6); *H. strophianus* (5.5); *H. viola* (5.4); *Heliodoxa aurescens* (6.4); *H. branickii* (5.2); *H. gularis* (6.3); *H. imperatrix* (8.8); *H. jacula* (8.2); *H. leadbeateri* (7.4); *H. rubinoides* (7.8); *H. schreibersii* (9.2); *H. xanthogonys* (7.0); *Heliomaster constantii* (7.3); *H. furcifer* (5.4); *H. longirostris* (6.6); *H. squamosus* (5.9); *Heliothryx aurita* (5.4); *H. barroti* (4.4); *Hylocharis chrysura* (4.5); *H. cyanus* (3.3); *H. eliciae* (3.6); *H. grayi* (5.6); *H. humboldtii* (6.2); *H. sapphirina* (4.4); *Hylonympha macrocerca* (7.3); *Klais guimeti* (2.6); *Lafresnaya lafresnayi* (5.3); *Lampornis amethystinus* (5.2); *L. calolaema* (4.9); *L. castaneoventris* (5.6); *L. cinereicauda* (5.6); *L. clemenciae* (7.6); *L. hemileucus* (5.5); *L. sybillae* (6.2); *L. viridipallens* (5.4); *Lamprolaima rhami* (7.8); *Lepidopyga coeruleogularis* (4.2); *L. goudoti* (4.0); *L. lilliae* (4.2); *Lesbia nuna* (3.7); *L. victoriae* (5.0); *Leucippus baeri* (4.5); *L. chionogaster* (5.1); *L. chlorocercus* (4.6); *L. fallax* (6.0); *L. taczanowskii* (6.4); *L. viridicauda* (6.1); *Leucochloris albicollis* (6.3); *Loddigesia mirabilis* (3.0); *Lophornis adorabilis* (2.7); *L. brachylophus* (2.8); *L. chalybeus* (3.0); *L. delattrei* (2.8); *L. gouldii* (2.4); *L. helenae* (2.6); *L. magnificus* (2.7); *L. ornatus* (2.3); *L. pavoninus* (3.0); *L. stictolophus* (2.2); *Metallura aeneocauda* (5.2); *M. baroni* (4.3); *M. eupogon* (4.6); *M. iracunda* (4.7); *M. odomae* (5.1); *M. phoebe* (5.4); *M. theresiae* (4.9); *M. tyrianthina* (3.9); *M. williami* (4.5); *Microchera albocoronata* (2.7); *Microstilbon burmeisteri* (2.5); *Myrmia micrura* (3.0); *Myrtis fanny* (2.3); *Ocreatus underwoodii* (3.0); *Opisthoprora euryptera* (4.8); *Oreonympha nobilis* (7.7); *Oreotrochilus adela* (6.6); *O. chimborazo* (8.2); *O. estella* (8.1); *O. leucopleurus* (6.4); *O. melanogaster* (9.1); *Oxypogon guerinii* (4.8); *Panterpe insignis* (5.7); *Patagona gigas* (20.2); *Phaethornis anthophilus* (5.9); *P. atrimentalis* (2.6); *P. augusti* (6.0); *P. baroni* (5.6); *P. bourcieri* (4.3); *P. eurynome* (5.3); *P. griseogularis* (2.3); *P. guy* (4.8); *P. hispidus* (5.0); *P. idaliae* (2.6); *P. koepckeae* (5.1); *P. longirostris* (6.0); *P. longuemareus* (3.0); *P. malaris* (5.9); *P. mexicanus* (8.4); *P. nattereri* (3.1); *P. philippii* (5.0); *P. pretrei* (5.6); *P. ruber* (2.4); *P. rupurumii* (3.7); *P. squalidus* (3.4); *P. striigularis* (3.0); *P. stuarti* (2.9); *P. subo-*

chraceus (3.8); *P. superciliosus* (6.3); *P. syrmatophorus* (5.8); *P. yaruqui* (5.4); *Phlogophilus harterti* (2.7); *P. hemileucurus* (2.8); *Polyonymus caroli* (4.8); *Polytmus guainumbi* (5.2); *P. milleri* (4.1); *P. theresiae* (3.8); *Pterophanes cyanopterus* (9.3); *Ramphodon naevius* (7.9); *Ramphomicron dorsale* (4.8); *R. microrhynchum* (3.6); *Rhodopis vesper* (3.8); *Sappho sparganura* (5.3); *Schistes geoffroyi* (4.0); *Selasphorus ardens* (2.4); *S. flammula* (2.7); *S. platycercus* (3.5); *S. rufus* (3.5); *S. sasin* (3.4); *S. scintilla* (2.2); *Sephanoides sephanoides* (5.2); *Stellula calliope* (2.7); *Stephanoxis lalandi* (4.0); *Sternoclyta cyanopectus* (8.0); *Taphrolesbia griseiventris* (8.1); *Taphrospilus hypostictus* (7.0); *Thalurania colombica* (4.5); *T. fannyi* (4.3); *T. furcata* (4.2); *T. glaucopis* (4.8); *T. hypochlora* (4.3); *T. ridgwayi* (3.8); *T. watertonii* (4.6); *Thaumastura cora* (1.9); *Threnetes niger* (5.6); *T. ruckeri* (5.2); *Tilmatura dupontii* (2.2); *Topaza pella* (12.2); *T. pyra* (12.7); *Urochroa bougueri* (11.4); *Urosticte benjamini* (3.9); *U. ruficrissa* (4.3); *Apaloderma aequatoriale* (49.0); *A. narina* (67.8); *A. vittatum* (55.0); *Euptilotis neoxenus* (123.0); *Harpactes diardii* (98.9); *H. duvaucelii* (39.1); *H. erythrocephalus* (80.3); *H. fasciatus* (62.0); *H. kasumba* (96.9); *H. oreskios* (57.3); *H. orrhophaeus* (53.3); *H. wardi* (119.0); *Pharomachrus antisianus* (153.0); *P. auriceps* (180.0); *P. fulgidus* (160.0); *P. mocinno* (203.0); *P. pavoninus* (163.0); *Trogon bairdii* (94.4); *T. caligatus* (130.0); *T. chionurus* (82.0); *T. citreolus* (79.0); *T. clathratus* (130.0); *T. collaris* (64.2); *T. comptus* (114.0); *T. curucui* (54.0); *T. elegans* (70.9); *T. massena* (141.0); *T. melanocephalus* (85.1); *T. melanurus* (114.0); *T. mesurus* (104.0); *T. mexicanus* (71.0); *T. personatus* (63.4); *T. rufus* (53.8); *T. surrucura* (73.3); *T. violaceus* (46.8); *T. viridis* (89.7); *Ortyxelos meiffrenii* (17.6); *Turnix castanota* (84.1); *T. hottentotta* (51.4); *T. maculosa* (39.6); *T. melanogaster* (87.9); *T. olivei* (81.3); *T. pyrrhothorax* (46.7); *T. suscitator* (50.5); *T. sylvatica* (54.3); *T. tanki* (53.4); *T. varia* (91.9); *T. velox* (45.0); *Agriornis andicola* (53.9); *A. livida* (99.2); *A. microptera* (67.8); *A. montana* (63.3); *Alectrurus risora* (32.7); *A. tricolor* (16.0); *Ampelioides tschudii* (78.4); *Ampelion rubrocristatus* (66.3); *A. rufaxilla* (73.9); *Anairetes alpinus* (9.0); *A. flavirostris* (6.0); *A. nigrocristatus* (13.8); *A. parulus* (6.2); *A. reguloides* (5.9); *Antilophia bokermanni* (19.8); *A. galeata* (21.5); *Aphanotriccus audax* (11.3); *A. capitalis* (11.8); *Arundinicola leucocephala* (13.8); *Attila bolivianus* (39.5); *A. cinnamomeus* (38.8); *A. citriniventris* (33.7); *A. phoenicurus* (32.3); *A. rufus* (42.6); *A. spadiceus* (39.1); *A. torridus* (46.0); *Calyptura cristata* (14.0); *Camptostoma imberbe* (7.4); *C. obsoletum* (8.1); *Capsiempis flaveola* (7.7); *Carpodectes antoniae* (98.0); *C. hopkei* (102.0); *C. nitidus* (116.0); *Carpornis cucullatus* (75.7); *C. melanocephalus* (64.2); *Casiornis fusca* (19.5); *C. rufa* (24.8); *Cephalopterus glabricollis* (385.0); *C. ornatus* (380.0); *C. penduliger* (338.0); *Chiroxiphia boliviana* (17.2); *C. caudata* (25.6); *C. lanceolata* (18.5); *C. linearis* (17.5); *C. pareola* (16.9); *Chloropipo flavicapilla* (17.8); *C. holochlora* (14.9); *C. unicolor* (15.5); *C. uniformis* (17.9); *Cnemarchus erythropygius* (38.1); *Cnemotriccus fuscatus* (13.6); *Cnipodectes subbrunneus* (23.2); *Colonia colonus* (18.3); *Colorhamphus parvirostris* (10.6); *Conioptilon mcilhennyi* (90.0); *Conopias albovittata* (24.4); *C. cinchoneti* (25.0); *C. parva* (21.0); *C. trivirgata* (16.7); *Contopus albogularis* (9.6); *C. cinereus* (11.6); *C. cooperi* (32.1); *C. fumigatus* (19.9); *C. lugubris* (21.5); *C. nigrescens* (9.5); *C. ochraceus* (23.0); *C. pertinax* (27.2); *C. punensis* (19.1); *C. sordidulus* (13.1); *C. virens* (13.9); *Corapipo gutturalis* (8.2); *C. leucorrhoa* (11.7); *Corythopis delalandi* (15.0); *C. torquata* (14.3); *Cotinga amabilis* (71.5); *C. cayana* (61.8); *C. cotinga* (54.0); *C. maculata* (65.0); *C. maynana* (69.0); *C. nattererii* (57.1); *C. ridgwayi* (57.3); *Culicivora caudacuta* (7.2); *Deltarhynchus flammulatus* (17.2); *Dixiphia pipra* (12.9); *Doliornis remseni* (63.1); *D. sclateri* (60.2); *Elaenia albiceps* (15.5); *E. chiriquensis* (15.3); *E. cristata* (18.2); *E. dayi* (30.0); *E. flavogaster* (24.8); *E. frantzii* (19.6); *E. gigas* (31.0); *E. martinica* (20.9); *E. mesoleuca* (17.8); *E. obscura* (23.9); *E. pallatangae* (17.8); *E. parvirostris* (13.8); *E. pelzelni* (26.9); *E. ruficeps* (18.6); *E. spectabilis* (27.3); *E. strepera* (19.3); *Empidonax affinis* (11.3); *E. albigularis* (9.7); *E. alnorum* (12.7); *E. atriceps* (9.0); *E. difficilis* (10.7); *E. flavescens* (12.5); *E. flaviventris* (11.8); *E. fulvifrons* (8.0); *E. hammondii* (10.5); *E. minimus* (10.0); *E. oberholseri* (10.4); *E. occidentalis* (11.6); *E. traillii* (13.4); *E. virescens* (12.6); *E. wrightii* (10.3); *Empidonomus varius* (27.1); *Euscarthmus meloryphus* (6.8); *E. rufomarginatus* (6.0); *Fluvicola albiventer* (11.6); *F. nengeta* (21.0); *F. pica* (12.3); *Griseotyrannus aurantioatrocristatus* (33.0); *Gubernetes yetapa* (68.4); *Gymnoderus foetidus* (283.0); *Haematoderus militaris* (227.0); *Hemitriccus cinnamomeipectus* (7.5); *H. diops* (10.0); *H. flammulatus* (10.0); *H. furcatus* (7.7); *H. granadensis* (7.9); *H. griseipectus* (7.9); *H. inornatus* (6.6); *H. iohannis* (10.0); *H. josephinae* (10.8); *H. kaempferi* (7.9); *H. margaritaceiventer* (8.4); *H. minimus* (7.0); *H. minor* (7.4); *H. mirandae* (7.2); *H. nidipendulus* (7.5); *H. obsoletus* (11.6); *H. orbitatus* (9.7); *H. rufigularis* (9.4); *H. spodiops* (7.2); *H. striaticollis* (8.6); *H. zosterops* (8.8); *Heterocercus aurantiivertex* (21.5); *H. flavivertex* (21.3); *H. linteatus* (21.2); *Hirundinea ferruginea* (30.6); *Hymenops perspicillatus* (22.9); *Ilicura militaris* (12.7); *Inezia caudata* (8.4); *I. inornata* (12.0); *I. subflava* (8.4); *I. tenuirostris* (5.0); *Iodopleura fusca* (15.5); *I. isabellae* (20.0); *I. pipra* (15.0); *Knipolegus aterrimus* (20.2);

K. cyanirostris (15.4); *K. franciscanus* (20.5); *K. hudsoni* (13.8); *K. lophotes* (31.8); *K. nigerrimus* (20.3); *K. orenocensis* (19.0); *K. poecilocercus* (14.3); *K. poecilurus* (14.6); *K. signatus* (17.8); *K. striaticeps* (11.0); *Laniisoma buckleyi* (48.0); *L. elegans* (47.4); *Laniocera hypopyrrha* (51.0); *L. rufescens* (48.1); *Lathrotriccus euleri* (11.4); *L. griseipectus* (11.0); *Legatus leucophaius* (22.2); *Lepidothrix coeruleocapilla* (9.1); *L. coronata* (10.7); *L. iris* (11.9); *L. isidorei* (7.9); *L. nattereri* (8.4); *L. serena* (16.8); *L. suavissima* (8.5); *L. vilasboasi* (8.4); *Leptopogon amaurocephalus* (11.7); *L. rufipectus* (13.4); *L. superciliaris* (11.7); *L. taczanowskii* (11.5); *Lessonia oreas* (13.8); *L. rufa* (13.4); *Lipaugus fuscocinereus* (138.0); *L. lanioides* (94.8); *L. streptophorus* (57.2); *L. unirufus* (82.1); *L. uropygialis* (116.0); *L. vociferans* (75.7); *L. weberi* (72.1); *Lophotriccus eulophotes* (6.0); *L. galeatus* (6.6); *L. pilaris* (6.8); *L. pileatus* (7.7); *L. vitiosus* (7.5); *Machaeropterus deliciosus* (12.7); *M. pyrocephalus* (9.7); *M. regulus* (9.4); *Machetornis rixosus* (29.6); *Manacus aurantiacus* (15.5); *M. candei* (19.9); *M. manacus* (15.0); *M. vitellinus* (18.2); *Masius chrysopterus* (11.6); *Mecocerculus calopterus* (7.0); *M. hellmayri* (8.0); *M. leucophrys* (11.0); *M. minor* (11.0); *M. poecilocercus* (7.7); *M. stictopterus* (9.4); *Megarynchus pitangua* (73.5); *Mionectes macconnelli* (13.5); *M. oleagineus* (10.8); *M. olivaceus* (15.5); *M. rufiventris* (13.3); *M. striaticollis* (15.0); *Mitrephanes olivaceus* (10.0); *M. phaeocercus* (8.6); *Muscigralla brevicauda* (12.6); *Muscipipra vetula* (27.0); *Muscisaxicola albifrons* (19.1); *M. albilora* (22.6); *M. alpina* (26.1); *M. capistrata* (26.6); *M. cinerea* (18.6); *M. flavinucha* (36.3); *M. fluviatilis* (14.7); *M. frontalis* (28.9); *M. grisea* (27.1); *M. juninensis* (22.2); *M. macloviana* (14.2); *M. maculirostris* (19.0); *M. rufivertex* (20.0); *Myiarchus apicalis* (29.2); *M. cephalotes* (26.4); *M. cinerascens* (28.2); *M. crinitus* (32.1); *M. ferox* (27.5); *M. nuttingi* (23.0); *M. panamensis* (31.7); *M. phaeocephalus* (26.3); *M. semirufus* (22.5); *M. swainsoni* (25.1); *M. tuberculifer* (18.2); *M. tyrannulus* (36.3); *M. venezuelensis* (29.8); *M. yucatanensis* (19.6); *Myiobius atricaudus* (10.0); *M. barbatus* (11.4); *M. mastacalis* (11.0); *M. sulphureipygius* (11.9); *M. villosus* (14.1); *Myiodynastes bairdii* (45.0); *M. chrysocephalus* (38.3); *M. hemichrysus* (43.4); *M. luteiventris* (46.9); *M. maculatus* (43.2); *Myiopagis caniceps* (10.2); *M. flavivertex* (11.9); *M. gaimardii* (12.2); *M. olallai* (12.1); *M. subplacens* (15.9); *M. viridicata* (12.3); *Myiophobus cryptoxanthus* (9.8); *M. fasciatus* (9.9); *M. flavicans* (12.7); *M. inornatus* (11.2); *M. lintoni* (9.8); *M. ochraceiventris* (10.5); *M. phoenicomitra* (11.0); *M. pulcher* (9.5); *M. roraimae* (13.7); *Myiornis albiventris* (4.9); *M. atricapillus* (5.7); *M. auricularis* (5.3); *M. ecaudatus* (5.3); *Myiotheretes fumigatus* (33.4); *M. fuscorufus* (31.7); *M. pernix* (30.0); *M. striaticollis* (61.2); *Myiotriccus ornatus* (13.5); *Myiozetetes cayanensis* (25.9); *M. granadensis* (29.3); *M. luteiventris* (19.0); *M. similis* (28.0); *Neopelma aurifrons* (14.0); *N. chrysocephalum* (15.5); *N. chrysolophum* (14.0); *N. pallescens* (18.2); *N. sulphureiventer* (15.9); *Neopipo cinnamomea* (7.7); *Neoxolmis rufiventris* (77.0); *Ochthoeca cinnamomeiventris* (12.0); *O. diadema* (11.5); *O. frontalis* (10.0); *O. fumicolor* (16.6); *O. jelskii* (11.6); *O. leucophrys* (13.1); *O. nigrita* (10.4); *O. oenanthoides* (17.7); *O. piurae* (10.6); *O. pulchella* (12.0); *O. rufipectoralis* (10.0); *O. spodionota* (10.7); *O. thoracica* (11.9); *Ochthornis littoralis* (13.4); *Oncostoma cinereigulare* (6.4); *O. olivaceum* (6.6); *Onychorhynchus coronatus* (14.0); *O. mexicanus* (21.0); *O. occidentalis* (22.7); *O. swainsoni* (17.0); *Ornithion brunneicapillum* (7.1); *O. inerme* (7.0); *O. semiflavum* (6.6); *Oxyruncus cristatus* (42.0); *Pachyramphus albogriseus* (17.3); *P. castaneus* (19.5); *P. cinnamomeus* (20.3); *P. major* (24.8); *P. marginatus* (19.2); *P. polychopterus* (20.8); *P. rufus* (18.8); *P. spodiurus* (18.2); *P. surinamus* (19.8); *P. versicolor* (15.5); *P. viridis* (21.0); *P. xanthogenys* (19.6); *Perissocephalus tricolor* (340.0); *Phaeomyias murina* (10.0); *P. tumbezana* (9.8); *Phelpsia inornata* (29.4); *Phibalura flavirostris* (46.5); *Philohydor lictor* (25.5); *Phoenicircus carnifex* (83.7); *P. nigricollis* (96.5); *Phyllomyias burmeisteri* (10.8); *P. cinereiceps* (9.9); *P. fasciatus* (10.5); *P. griseiceps* (7.6); *P. griseocapilla* (9.1); *P. nigrocapillus* (9.5); *P. plumbeiceps* (9.6); *P. reiseri* (9.8); *P. sclateri* (9.9); *P. urichi* (7.5); *P. uropygialis* (8.7); *P. virescens* (11.0); *P. zeledoni* (10.9); *Phylloscartes beckeri* (8.7); *P. ceciliae* (7.6); *P. difficilis* (6.9); *P. flaviventris* (8.0); *P. flavovirens* (8.8); *P. gualaquizae* (8.0); *P. kronei* (8.3); *P. nigrifrons* (9.1); *P. oustaleti* (10.0); *P. parkeri* (8.1); *P. paulistus* (7.5); *P. roquettei* (6.0); *P. superciliaris* (7.8); *P. sylviolus* (6.6); *P. ventralis* (8.3); *P. virescens* (8.5); *Phytotoma raimondii* (39.8); *P. rara* (47.0); *P. rutila* (40.5); *Pipra aureola* (16.2); *P. chloromeros* (16.5); *P. cornuta* (25.3); *P. erythrocephala* (13.5); *P. fasciicauda* (15.9); *P. filicauda* (15.4); *P. mentalis* (15.0); *P. rubrocapilla* (12.0); *Pipreola arcuata* (118.0); *P. aureopectus* (46.0); *P. chlorolepidota* (29.5); *P. formosa* (47.2); *P. frontalis* (42.4); *P. intermedia* (47.9); *P. jucunda* (53.8); *P. lubomirskii* (45.5); *P. pulchra* (58.2); *P. riefferii* (49.3); *P. whitelyi* (50.0); *Piprites chloris* (16.0); *P. griseiceps* (16.0); *P. pileatus* (15.0); *Pitangus sulphuratus* (63.3); *Platypsaris aglaiae* (30.0); *P. homochrous* (35.0); *P. minor* (37.0); *P. validus* (28.8); *Platyrinchus cancrominus* (9.2); *P. coronatus* (9.2); *P. flavigularis* (10.0); *P. leucoryphus* (16.0); *P. mystaceus* (9.7); *P. platyrhynchos* (12.0); *P. saturatus* (10.7); *Poecilotriccus albifacies* (8.0); *P. calopterus* (7.6); *P. capi-*

talis (8.0); *P. fumifrons* (6.6); *P. latirostris* (8.1); *P. luluae* (7.3); *P. plumbeiceps* (7.4); *P. pulchellus* (7.4); *P. ruficeps* (9.1); *P. russatus* (7.4); *P. senex* (7.3); *P. sylvia* (7.1); *Pogonotriccus chapmani* (7.5); *P. eximius* (6.8); *P. lanyoni* (8.0); *P. ophthalmicus* (11.0); *P. orbitalis* (7.4); *P. poecilotis* (8.0); *P. venezuelanus* (9.0); *Polioxolmis rufipennis* (34.5); *Polystictus pectoralis* (6.2); *P. superciliaris* (6.0); *Porphyrolaema porphyrolaema* (60.0); *Procnias alba* (210.0); *P. averano* (148.0); *P. nudicollis* (174.0); *P. tricarunculata* (11.9); *Pseudelaenia leucospodia* (11.9); *Pseudocolopteryx acutipennis* (6.9); *P. dinellianus* (6.6); *P. flaviventris* (7.5); *P. sclateri* (8.0); *Pseudotriccus pelzelni* (10.9); *P. ruficeps* (11.3); *P. simplex* (9.5); *Pyrocephalus rubinus* (14.4); *Pyroderus scutatus* (357.0); *Pyrrhomyias cinnamomea* (10.8); *Querula purpurata* (108.0); *Ramphotrigon fuscicauda* (18.6); *R. megacephala* (14.2); *R. ruficauda* (18.4); *Rhynchocyclus brevirostris* (24.3); *R. fulvipectus* (23.1); *R. olivaceus* (21.3); *R. pacificus* (19.2); *Rhytipterna holerythra* (36.8); *R. immunda* (27.4); *R. simplex* (31.8); *Rupicola peruviana* (244.0); *R. rupicola* (195.0); *Satrapa icterophrys* (21.5); *Sayornis nigricans* (18.7); *S. phoebe* (20.0); *S. saya* (20.9); *Schiffornis major* (31.0); *S. turdinus* (31.7); *S. virescens* (25.6); *Serpophaga cinerea* (8.3); *S. griseiceps* (9.8); *S. hypoleuca* (6.1); *S. munda* (5.4); *S. nigricans* (8.5); *S. subcristata* (6.6); *Sirystes albogriseus* (32.0); *S. sibilator* (32.3); *Stigmatura bahiae* (14.0); *S. budytoides* (11.2); *S. gracilis* (11.4); *S. napensis* (9.8); *Sublegatus arenarum* (12.3); *S. modestus* (14.0); *S. obscurior* (16.0); *Suiriri affinis* (15.3); *S. islerorum* (22.8); *S. suiriri* (14.6); *Tachuris rubrigastra* (7.8); *Taeniotriccus andrei* (9.5); *Terenotriccus erythrurus* (7.4); *Tijuca atra* (163.0); *T. condita* (80.0); *Tityra cayana* (68.1); *T. inquisitor* (43.1); *T. semifasciata* (79.3); *Todirostrum chrysocrotaphum* (7.0); *T. cinereum* (6.3); *T. maculatum* (7.3); *T. nigriceps* (6.5); *T. pictum* (6.8); *T. poliocephalum* (6.9); *T. viridanum* (6.9); *Tolmomyias assimilis* (17.0); *T. flaviventris* (12.2); *T. flavotectus* (15.7); *T. poliocephalus* (10.8); *T. sulphurescens* (14.8); *T. traylori* (11.5); *T. viridiceps* (11.3); *Tumbezia salvini* (12.2); *Tyranneutes stolzmanni* (7.2); *T. virescens* (7.2); *Tyrannopsis sulphurea* (53.6); *Tyrannulus elatus* (7.0); *Tyrannus albogularis* (37.1); *T. couchii* (39.0); *T. crassirostris* (55.9); *T. dominicensis* (46.5); *T. forficatus* (39.3); *T. melancholicus* (37.4); *T. niveigularis* (34.4); *T. savana* (31.9); *T. tyrannus* (40.0); *T. verticalis* (39.6); *T. vociferans* (45.6); *Uromyias agilis* (13.9); *U. agraphia* (12.5); *Xenopipo atronitens* (15.6); *Xenopsaris albinucha* (19.5); *Xenotriccus callizonus* (11.2); *X. mexicanus* (13.8); *Xipholena atropurpurea* (61.5); *X. lamellipennis* (70.9); *X. punicea* (68.1); *Xolmis cinerea* (57.1); *X. coronata* (46.8); *X. dominicana* (42.8); *X. irupero* (28.7); *X. murina* (33.4); *X. pyrope* (35.3); *X. rubetra* (36.3); *X. salinarum* (25.1); *X. velata* (35.5); *Zaratornis stresemanni* (52.1); *Zimmerius bolivianus* (11.0); *Z. chrysops* (10.4); *Z. cinereicapillus* (11.8); *Z. flavidifrons* (10.5); *Z. gracilipes* (7.2); *Z. improbus* (10.9); *Z. vilissimus* (9.2); *Z. villarejoi* (6.6); *Z. viridiflavus* (9.6); *Phodilus badius* (282.0); *Tyto alba* (350.0); *T. capensis* (381.0); *T. longimembris* (342.0); *T. multipunctata* (464.0); *T. novaehollandiae* (645.0); *T. tenebricosa* (690.0); *Upupa epops* (65.7); *Cyclarhis gujanensis* (28.8); *C. nigrirostris* (31.9); *Hylophilus amaurocephalus* (10.0); *H. aurantiifrons* (9.5); *H. brunneiceps* (9.9); *H. decurtatus* (8.5); *H. flavipes* (11.7); *H. hypoxanthus* (17.0); *H. muscicapinus* (11.7); *H. ochraceiceps* (11.6); *H. olivaceus* (12.0); *H. pectoralis* (11.6); *H. poicilotis* (10.4); *H. sclateri* (11.2); *H. semibrunneus* (11.4); *H. semicinereus* (13.0); *H. thoracicus* (13.8); *Vireo altiloquus* (19.0); *V. atricapillus* (9.0); *V. bellii* (8.5); *V. brevipennis* (11.8); *V. carmioli* (13.1); *V. cassinii* (14.7); *V. flavifrons* (18.0); *V. flavoviridis* (17.6); *V. gilvus* (12.7); *V. griseus* (11.4); *V. huttoni* (11.3); *V. hypochryseus* (12.2); *V. leucophrys* (12.3); *V. magister* (15.4); *V. masteri* (11.2); *V. nelsoni* (9.4); *V. olivaceus* (16.2); *V. pallens* (11.0); *V. philadelphicus* (11.5); *V. plumbeus* (16.4); *V. solitarius* (15.3); *V. vicinior* (12.8); *Vireolanius eximius* (17.5); *V. leucotis* (26.0); *V. melitophrys* (34.7); *V. pulchellus* (24.0); *Zosterops abyssinica* (11.0); *Z. erythropleura* (11.0); *Z. everetti* (10.0); *Z. japonicus* (11.5); *Z. lateralis* (12.7); *Z. luteus* (9.7); *Z. pallidus* (9.3); *Z. palpebrosus* (8.6); *Z. poliogaster* (11.0); *Z. senegalensis* (10.6); *Chloropeta gradcilirostris* (11.5); *Schistolais leontica* (12.0); *Buteo auger* (953.2); *B. archeri* (830.5); *Ploceus heuglini* (25.7); *P. quadricinctus* (218.8); *Turdoides fulvus* (60.0); *C. sanguinea* (450.0); *Petrophassa albipennis* (203.6); *S. seloputo* (1293.0);

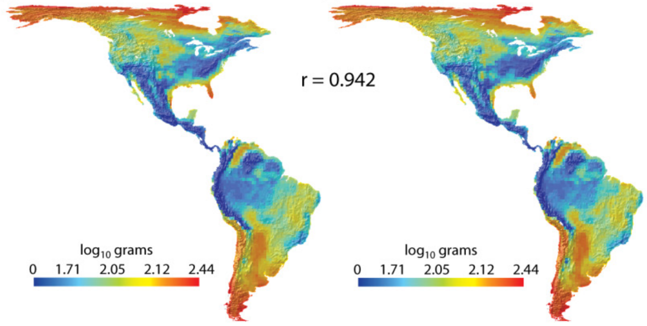
Appendix S2

Table S2. Comparison of PVR's-estimated phylogenetic signals in log10 body size between family, genus and species levels for the New World mammals. The analysis was based on the species-level supertree of Bininda-Emonds *et al.* (2007) without including branch lengths (to match the structure of the tree employed for birds in the present study) and collapsed to decreasing levels of resolution from species to genera to families. For each level, we applied the same protocol described in the Methods for birds in order to generate and select representative phylogenetic eigenvectors for body size variation across the phylogeny with PVR. As for the case of birds, the amount of phylogenetic signal in mammal body size captured at the family level is very high (79%), whereas increasing the taxonomic resolution to the species level only added an extra 5.8%. Although this is indirect evidence obtained from a different endothermic group, it supports our use of a family level phylogeny to studying bird body size patterns.

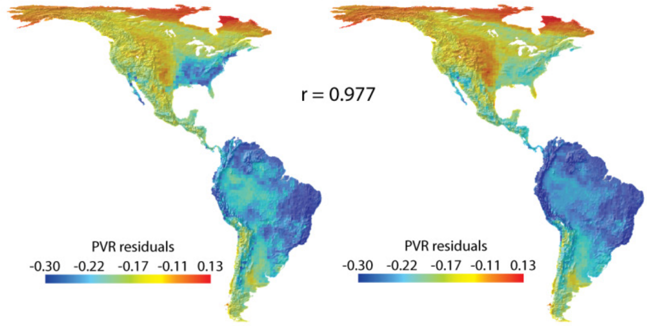
Taxonomic level	Number of taxa	Number of eigenvectors	PVR's-R^2
Family	49	9	0.787
Genus	269	26	0.837
Species	1109	34	0.845

Appendix S3

Figure S1. To establish if our results are affected by the use of nodes instead of branch lengths as the measure for phylogenetic distances, we compared the use of both methods in the New World. We used Sibley and Alquist (1990) phylogeny. We extracted two pairwise phylogenetic distance matrices, which were calculated using node counting (NC) and branch lengths (BL). We performed PVR at the family level for each phylogenetic distance matrix in order to compare the mean PA- and PI-components and to determine whether our results are robust to the use of either method. Associations between the mean PA-components of a branch length phylogeny (a) and a node counting phylogeny (b) (r=0.942), and between the mean PI-components for a branch length phylogeny (c) and a node counting phylogeny (d) (r=0.977) are very strong. Thus, the use of node counting instead of branch lengths to determine phylogenetic distances among pairs of species does not influence our results.


(a) Mean PA-component BL

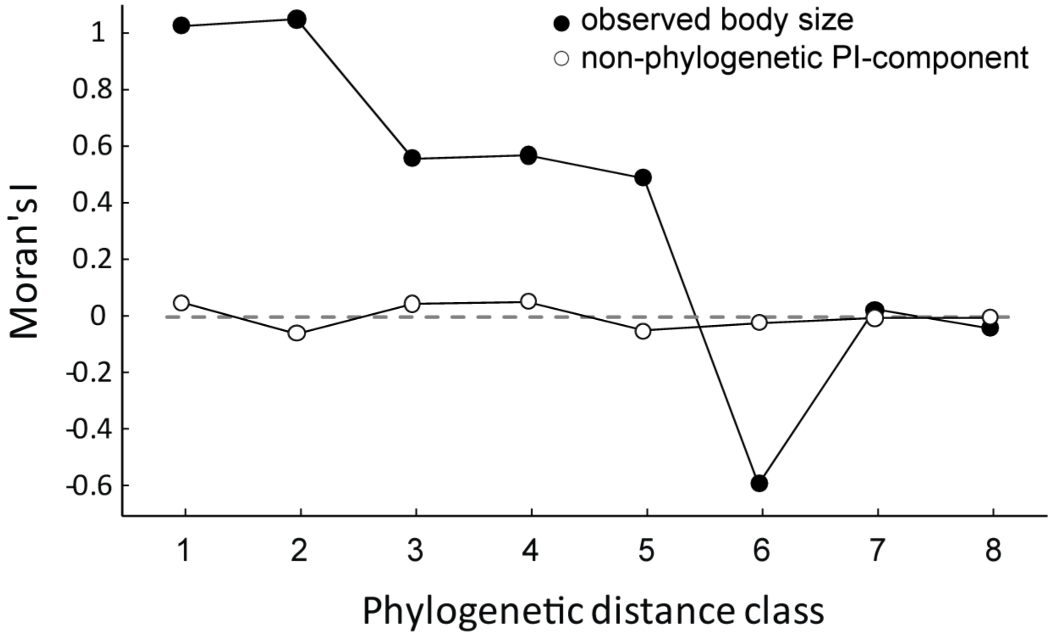
(b) Mean PA-component NC


(c) Mean PI-component BL

(d) Mean PI-component NC

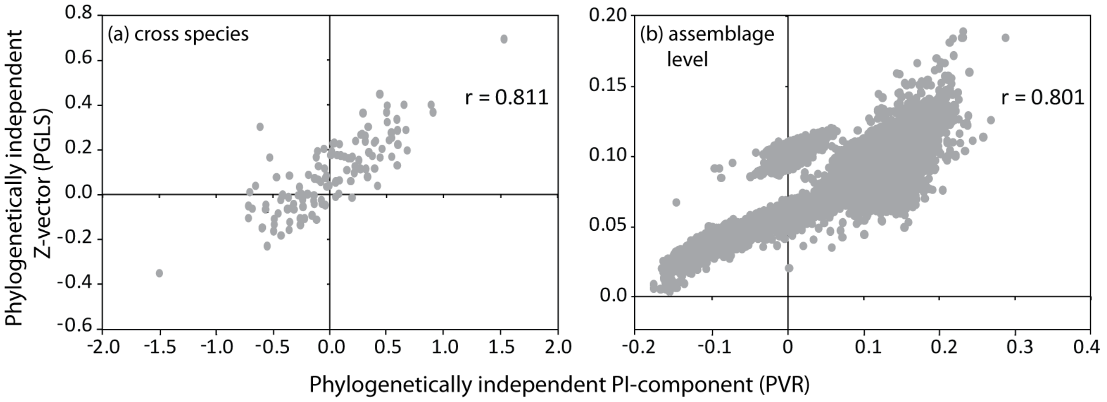
Appendix S4

Figure S2. Phylogenetic correlograms showing Moran's I coefficients for the body size of 122 bird families (solid circles). Coefficients were calculated using the phylogenetic distance matrix resulting from the combined phylogeny of Sibley and Ahlquist (1990) for non-passerines and Barker *et al.* (2004) phylogeny for passerines. Moran's I coefficients are also shown for the non-phylogenetic PI-component of each of the 122 bird families (empty circles), indicating absence of autocorrelation in such component and thus independence from phylogeny.

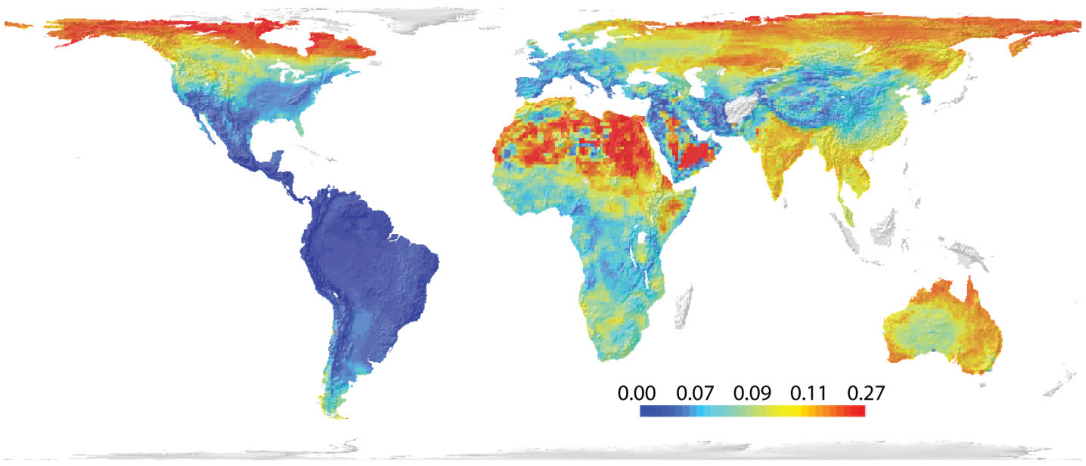


Appendix S5

Figure S3. Comparison between a PGLS transform of mean family log10-body size (Z-vector) and the PI component given by PVR. The Z-vector was computed following Diniz-Filho *et al.* (2011) and showed minimal phylogenetic autocorrelation (Moran's I=0.014 for the first phylogenetic distance class), as it was also the case for the PI component (see Fig. S2). Bird family values of both metrics were highly correlated (a), and the correlation was similar when comparing their mean values in the cells globally (b). This resulted in a strong similarity between the map of mean Z-vector values (c) and that obtained for the mean-PI (see Fig. 1c).

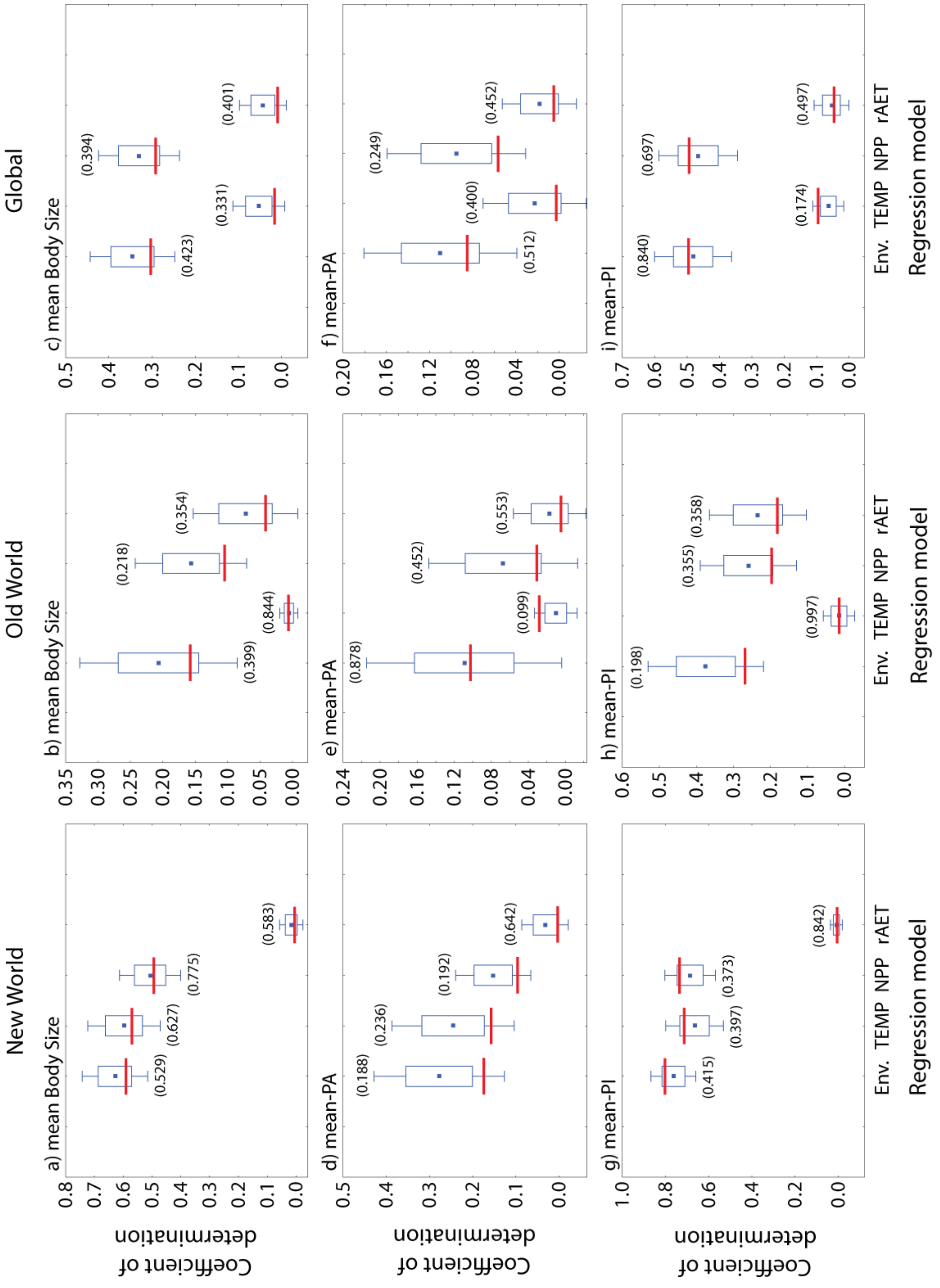


(c) Mean Z-vector (PGLS)



Appendix S6

Figure S4. Tests of potential influence of spatial autocorrelation on coefficients of determination of environmental OLS regressions for mean cell log10 body size, mean-PA and mean-PI in the New World (4,001 cells), Old Wold (8,638 cells), and globally (12,639 cells). Two types of coefficients of determination are included for comparison: coefficients obtained from whole data sets (red lines), and averaged coefficients (blue symbols: mean value ±1 SD, and ±1.96 SD) across sets of 100 subsamples generated for each region so that positive spatial autocorrelation was minimized in each subsample by randomly selecting cells (New and Old Wolds: 50 cells per sample; global extent: 100 cells) constrained to be separated at least 1,000 km (Moran's I ≤ 0.2 beyond that distance). Results for multiple regressions including TEMP, NPP and rAET (Env.) and simple regressions involving these variables are presented. Numbers in parentheses are p-values from t-tests comparing coefficients of determination fro m whole datasets and averaged coefficients from randomized subsample sets. As can be seen, no significant differences were found in any case, confirming that spatial autocorrelation does not bias OLS regression coefficients.


New World
Old World
Global
Coefficient of determination
a) mean Body Size
b) mean Body Size
c) mean Body Size
d) mean-PA
e) mean-PA
f) mean-PA
g) mean-PI
h) mean-PI
i) mean-PI
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0.24
0.16
0.12
0.08
0.04
1.0
(0.529)
(0.627)
(0.775)
(0.583)
(0.399)
(0.844)
(0.218)
(0.354)
(0.423)
(0.331)
(0.394)
(0.401)
(0.188)
(0.236)
(0.192)
(0.642)
(0.878)
(0.099)
(0.452)
(0.553)
(0.512)
(0.400)
(0.249)
(0.452)
(0.415)
(0.397)
(0.373)
(0.842)
(0.198)
(0.997)
(0.355)
(0.358)
(0.840)
(0.174)
(0.697)
(0.497)
Env. TEMP NPP rAET
Regression model

5. Cenozoic migrations and the New World mammal body size gradient

Ignacio Morales-Castilla, Miguel Á. Rodríguez & Bradford A. Hawkins

Article submitted to *Ecography (In review)*

Capítulo 5

Huella de las migraciones cenozoicas y la historia evolutiva en el gradiente biogeográfico de tamaño corporal de mamíferos del Nuevo Mundo

Este capítulo reproduce íntegramente el texto del siguiente manuscrito:

MORALES-CASTILLA, I., OLALLA-TÁRRAGA, M. Á., PURVIS, A., HAWKINS, B. A. and RODRÍGUEZ, M. Á., The imprint of Cenozoic migrations and evolutionary history on the biogeographic gradient of body size in New World mammals. (*Ms. In preparation)*

Resumen

Los patrones biogeográficos son el resultado de la ecología, la evolución y los eventos históricos, aunque pocos estudios han abordado estas cuestiones de forma integrada. Aquí nos centramos en estudiar cómo los intercambios bióticos de mamíferos del final del Cenozoico han contribuido a configurar sus patrones geográficos de tamaño corporal contemporáneos en el Nuevo Mundo. En concreto, exploramos diferencias en los patrones de autocorrelación filogenética y en las asociaciones con las condiciones ambientales actuales entre los grupos que participaron y los que no participaron en intercambios bióticos pasados. Tanto las asociaciones con variables ambientales como la señal filogenética fue mayor para los grupos de mamíferos que participaron en las migraciones que para los grupos nativos. Nuestros resultados se pueden interpretar en base a la cantidad de tiempo del que han dispuesto los distintos clados para diversificarse y ocupar distintos nichos. Además, este trabajo identifica el papel de eventos históricos como las migraciones del Cenozoico en la configuración de los patrones actuales de tamaño corporal de mamíferos, y además nos permite indicar dónde dichas influencias han sido más fuertes para los mamíferos del Nuevo Mundo.

The imprint of Cenozoic migrations and evolutionary history on the biogeographic gradient of body size in New World mammals

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Abstract

Ecology, evolution and historical events all contribute to biogeographic patterns, but studies integrating them are scarce. Here we focus on how biotic exchanges of mammals during the Late Cenozoic have contributed to current geographic body size patterns. We explore differences in the environmental correlates and phylogenetic patterning of body size between the groups of mammals participating and not participating in past biotic exchanges. Both body size's association with environmental predictors and its phylogenetic signal were stronger for immigrated groups than for indigenous groups. Our results can be interpreted based on the length of time that clades have had to diversify and occupy niche space. Moreover, this work identifies a role for historical events such as Cenozoic migrations on configuring contemporary mammal body size patterns and illustrates where such influences have been strongest for New World mammals.

Introduction

Body size patterns of mammals have been extensively studied in macroecology and macroevolution. One recurring theme has been to explain ecogeographic rules through comparative associations between body size and contemporary climatic conditions (Rodríguez *et al.* 2006, 2008, Diniz-Filho *et al.* 2009). For example, Rodríguez *et al.* (2008) documented assemblage-level patterns of body size across the New World and detected a body size gradient consistent with Bergmann's rule (i.e. larger average size in colder areas) in the Nearctic but a reversed pattern in the Neotropics. A contrasting approach has been to investigate mammalian body size patterns from an evolutionary perspective, to determine which models better explain body size evolution (Cooper & Purvis 2010), when maximum body sizes were reached (Smith *et al.* 2010), or whether body size influences conservatism of climatic niches (Cooper *et al.* 2011). Furthermore, the strength of the phylogenetic signal in mammal body size has been investigated either as opposed to spatial signal in an evolutionary modeling context (Freckleton & Jetz 2009) or as a way to define geographical patterns in independent adaptation (Diniz-Filho *et al.* 2009).

Historical processes such as past biotic exchanges or Pleistocene glaciations have also been suggested as possible drivers for mammal body size patterns (Marquet & Cofré 1999; Blackburn & Hawkins 2004; Rodríguez *et al.* 2006). Accordingly, large-scale migratory movements of mammals in the Pliocene and Pleistocene, either between the American continents (i.e., the Great American Biotic Interchange, GABI) or from Eurasia to the Americas (Marshall 1988, Webb & Barnosky 1989, Marquet and Cofré 1999, Woodburne *et al.* 2006, Cody *et al.* 2010) in which mainly large-sized clades were involved (Bowman *et al.* 2002), might be expected to have left an imprint on current mammal body size gradients. Nonetheless, the potential influence of non-indigenous clades on the current geographical body size patterns of mammals is unknown.

Here, we expand the assemblage-level analyses of Rodríguez *et al.* (2008) by explicitly considering evolutionary and historical factors related to the body size gradient of non-volant mammals in the New World. To document the influence of historical migrations on body size gradients, we separately analyze body size patterns of allochthon and autochthon species (i.e., those belonging or not belonging, respectively, to genera arriving through Pliocene-Pleistocene biotic exchanges) and compare them to the overall gradient across all species. We investigate associations of the body size of the different groups (i.e., all species, autochthons and allochthons) with ecological hypothesis for body size represented by a set of environmental predictors. To determine the extent to which body size patterns are influenced by phylogenetic autocorrelation we use process-based phylogenetic metrics as Blomberg's *et al.* (2003) K statistic or Pagel's (1999) λ. We also use pattern-based metrics such as Moran's I (Gittleman & Kot 1990) which allow us to assess variation of phylogenetic signal at different distances. Because we acknowledge that there might be other influences on spatial variation in the patterns of body size, we also account for the spatial variation in body size that is unrelated to the ecological hypotheses.

Marquet and Cofré (1999) identified the GABI as a key event on configuring the patterns in the statistical distribution of mammal body size in South America. Therefore, we expect to find strong influence of allochthon clades on geographical body size patterns. We also hypothesize that evolutionary time must play a role in adaptation by clades to macroclimatic conditions through macroevolution, derived from the time-for-speciation effect (Stephen & Wiens 2003). It has been shown that in more climatically stable areas, clades of different taxa find more opportunities to adapt, occupy different niches and diversify (Carnaval *et al.* 2009, Hortal *et al.* 2011). In contrast, clades evolving in climatically unstable areas (i.e., areas that were glaciated in the Pleistocene, or analogously, allochthon clades that have spent reduced periods of time in 'recently' colonized areas) would have less time to occupy the ecological niche space (e.g., Peterson 2011). In that case, macroclimate would act as a filter leading allochthon clades to occupy only the suitable climatic niches to which they were previously adapted (Hawkins *et al.* 2006, 2007). Based on the assumption that allochthons arrived more recently in North America or South America than autochthons and have thus had less time to diversify, we make two predictions. First, we predict a stronger signature of macroclimate on the body size of allochthon clades simply because autochthon clades would have had more time to adapt and fill different niches. Second, we predict stronger phylogenetic signal (i.e., phylogenetic niche conservatism) in the body size of allochthons than in the body size of autochthons. That prediction may also arise from the fact that allochthons are formed by the nonrandom subset of clades that participated in biotic exchanges; these clades are likely to have broadly similar dispersal ability (Phillimore *et al.* 2006), which has been linked to body size (Bowman *et al.* 2002).

If the abovementioned predictions are true, then we would expect allochthons to be unevenly distributed and thus, to have a different relative influence over the body size pattern of all species in different regions. This is based on the idea of habitat tracking, which has been recently shown for neogene mammals (Raia *et al.* 2011). In sum, if allochthon clades distributions are filtered by macroclimatic conditions, if they show strong phylogenetic signal for body size and if they show some degree of niche conservatism, then their contemporary distributions should be related to the environmental conditions to which they were adapted prior to migrating.

Material and Methods

The data

Range maps for all New World non-volant terrestrial mammal species were extracted from Schipper *et al.* (2008) and rasterized in a Behrmann equal-area 9,319 km^2 grid comprising 3,966 cells. After cross-comparison with the latest mammal taxonomy (Wilson & Reeder 2005) and with species included in Bininda-Emonds *et al.*'s (2007, 2008) phylogeny, a total of 1,109 species were considered for analysis (Appendix 1). Body mass (in grams) for each species was compiled from the PanTHERIA database (Jones *et al.* 2009), and for 14 species (1.2% of all species) for which we could not find direct measures of size, we assigned the average mass of its genus. Body masses were $\log_{10}$-transformed for analysis.

Originations in a given continent or region consist of new evolutionary branches (autochthons) and new immigrants (allochthons); according to Webb & Barnosky (1989), the distinction between allochthons and autochthons in the New World's mammal fauna usually can be made with confidence for the relatively complete records of the late Cenozoic genera (see Webb & Barnosky 1989; Woodburne *et al.* 2006). Thus, to investigate the influence of migrations on body size gradients, we divided our database into groups of species differentiated by the continent of origin of each genus (see Appendix 1). We identified 429 species belonging to 225 genera native to North America (hereafter NA-autochthons) and 322 species belonging to 145 genera native to South America (SA-autochthons). Also, allochthons in North America belonged to two groups depending on whether they belonged to genera that migrated from Eurasia in the Plio-Pleistocene (Eurasian-allochthons: 56 species, 17 genera), or from South America during the Great American Biotic Interchange (GABI-allochthons of NA: 19 species, 16 genera). Finally, most South American allochthons belonged to genera native to North America that colonized South America during the GABI (GABI-allochthons of SA: 347 species, 124 genera). Although a handful of Eurasian genera also arrived in South America during this event, we did not analyze this group due to the small sample size (7 species in 3 genera).

Environmental variables were used to assess four hypotheses previously identified as probable, not mutually exclusive (e.g. Olson *et al.* 2009) explanations of geographic mammal body size patterns. (1) The *heat conservation hypothesis* – larger endotherms abound in colder areas due to their lower surface-area-to-volume ratio and thus larger capability to preserve body heat (Bergmann 1847) – was investigated using Mean Annual Temperature (Bio 1 from WorldClim, Hijmans *et al.* 2005). (2) The *resource availability hypothesis* – more productive environments lead to larger body sizes because resource availability sets a limit to the body size an animal can reach (Rosenzweig 1968, Geist 1987) – was explored using annual average Net Primary Productivity (NPP) extracted from Imhoff *et al.* (2004) (data available at: http://sedac.ciesin.columbia.edu/es/hanpp.html; last accessed on March 2011). (3) The *resistance to starvation hypothesis* (or *fasting endurance*) – larger animals are favoured in less productive and more seasonal environments because they metabolize fat stores at lower weight-specific rates and, thus, cope with starvation better than smaller animals (Calder, 1984; Lindstedt & Boyce, 1985; Cushman *et al.*, 1993) – was also assessed based on NPP, but in this case predicting negative covariation with body size. And (4) the *habitat availability hypothesis* – the finer habitat zonation associated with stronger mesoscale climatic gradients in tropical mountains limits the occurrence of large species (Hawkins & Diniz-Filho, 2006; Rodríguez *et al.* 2008) – was assessed using range in elevation (data available at: http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htm; last accessed on January 2011) as our indicator of variation in mesoclimate (see Rodríguez *et al.* 2008 for details). All variables were rescaled and binned within each cell in our grid for analyses. Additionally we also computed the number of species in each cell and mapped species richness for each group of mammals (Appendix 2).

Environmental correlates of body size

The hypotheses linking body size to the environmental variables were evaluated with saturated multiple OLS regression models of the observed mean log-transformed body sizes for each group (all species, autochthons and Eurasian and GABI allochthons). As the hypothesis are not mutually exclusive, the environmental variables linked to them are not orthogonal ($r_{\mathrm{TEMP\ vs.\ NPP}} = 0.615$, $r_{\mathrm{TEMP\ vs.\ RIE}} = 0.038$, and $r_{\mathrm{NPP\ vs.\ RIE}} = 0.179$ in the Nearctic and $r_{\mathrm{TEMP\ vs.\ NPP}} = 0.766$, $r_{\mathrm{TEMP\ vs.\ RIE}} = 0.558$, and $r_{\mathrm{NPP\ vs.\ RIE}} = 0.469$ in the Neotropics). To evaluate the influence of collinearity on the stability of the standardized regression coefficients we computed both the condition number (CN) and the variance inflation factors (VIFs) of the models, assuming that values of VIF lower than 10 and a CN lower than 5 indicate that collinearity is not a major problem (see Olalla-Tárraga *et al.* 2009 for details). Analyses were done separately for the Nearctic and Neotropics biogeographic regions (Cox 2001) due to their different evolutionary histories (Laurasia vs. Gondwana) and geographic patterns of mammal body size variation (Rodríguez *et al.* 2008).

Data in macroecology are spatially structured, so we expected strong spatial autocorrelation in both mean $\log_{10}$-body sizes and environmental predictors. The spatial structure in body size represents the pattern we are trying to explain, although regression models including only three environmental predictors are likely to result in spatially autocorrelated residual variation. This would impact statistical inference if we used significance tests for variable evaluation, but we circumvented this issue by focusing our interpretations on the regression coefficients of the OLS models, which are not biased by residual autocorrelation (Cressie 1993, Fortin and Dale 2005, Schabenberg and Gotway 2005). However, we also quantified spatial autocorrelation in model residuals to evaluate the extent to which the environmental variables (and their associated hypothesis) might underlie the observed body size patterns. For this we generated sets of spatial filters describing the spatial variation in body size variables that is independent from the spatial variation already explained by the environmental predictors. We selected spatial filters for each response variable (i.e., the mean $\log_{10}$-body size of all species, GABI allochthons, Eurasian allochthons and autochthons in both the Nearctic and the Neotropics) using the algorithm proposed by Griffith & Peres-Neto (2006). This method selects the set of eigenvectors that describe all the variation in a given trait that is spatially autocorrelated above certain threshold (residual Moran's $I \leq 0.05$ in this case). We first regressed body size against the set of spatial eigenvectors. Subsequently, the amount of variation in the trait that is spatially structured, as predicted by the set of eigenvectors, was regressed against the environmental predictors. We then used the residuals of this second regression as a predictor in OLS regressions for body size (in combination with environmental predictors) in order to account for the spatial structure of the trait that is independent from the spatial structure explained by environmental variables (see Appendix 6 for details). We used Moran's I spatial correlograms (not shown) to confirm whether this approach removed the spatial autocorrelation of the residuals of our multiple-regression models at all distance classes.

Because relationships of mammal body size with temperature are non-linear, with body size increasing as temperature falls below a threshold of 10.9 °C in the Nearctic and 12.6 °C in the Neotropics (Rodríguez *et al.* 2008), we investigated such relationships by fitting lowess regression lines. We visually inspected body size vs. temperature scatterplots and reported only those for which non-linearity was found (i.e all species and allochthon species) (Appendix 4). We recalculated OLS models below and above the temperature for which body size-temperature relationships shifted (*ca.* 11 °C, Appendix 5).

Phylogenetic autocorrelation analyses

We used the 'best dates' phylogenetic supertree from Bininda-Emonds *et al.* (2007, 2008) to compute amounts of phylogenetic signal in the cross-species variation of body sizes for all the species in our database and for the groups of autochthon and allochthon species, pruning the tree in each case to include the species involved in each analysis. Phylogenetic signal was first calculated using Pagel's (1999) λ, which varies from 0 (no phylogenetic signal) to 1 (compatible with Brownian Motion, BM). Likelihood ratios were used to test whether λ was significantly different from 1.0

(Cooper *et al.* 2010). Because values of λ > 1.0 are not defined (Freckleton *et al.* 2002, Revell *et al.* 2008), the metric is unable to detect phylogenetic signal stronger than BM; we therefore also calculated Blomberg's K statistic (Blomberg *et al.* 2003). K ranges from 0 to ∞, with values <1.0 indicating low phylogenetic signal, values equal to 1.0 Brownian Motion, and values >1.0 a stronger phylogenetic signal than the neutral expectation. The statistical significance of K was tested by randomization of the data among species. For both Pagel's λ and Blomberg's K polytomies in the phylogeny were resolved randomly by zero-length branches. We used R v. 2.10.1 (R Development Core Team 2009) to compute both metrics. Lastly, we inspected Moran's *I* correlograms to explore the patterns of phylogenetic autocorrelation at different depths of the phylogeny (Machac *et al.* 2011) (see Appendix 2).

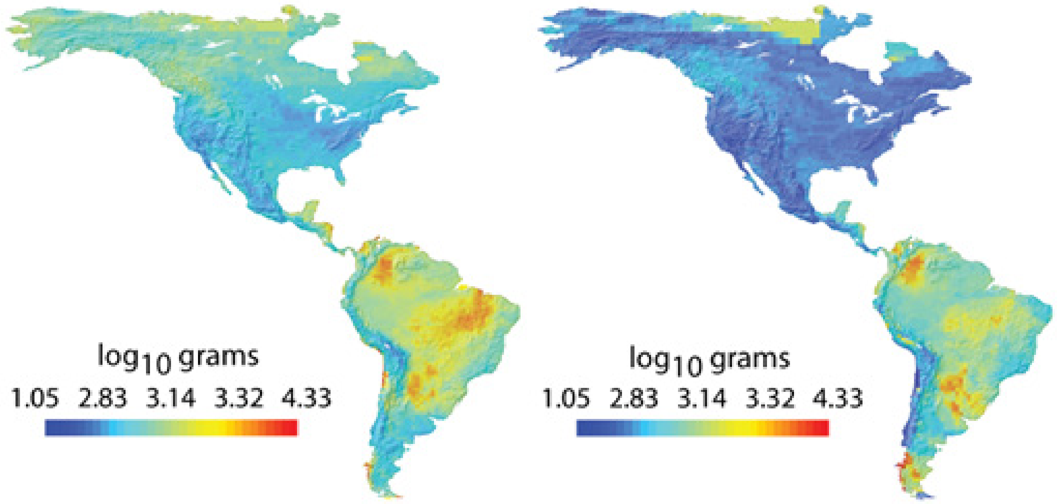
Results

Geographical patterns in body size

The geographical patterns of body size of all species were virtually identical to those reported by Rodríguez *et al.* (2008) even though our database comprised fewer species (i.e., only those included in Bininda-Emonds *et al.* [2007, 2008] supertree). In the Nearctic, a Bergmannian latitudinal gradient was found, whereas in the Neotropics, large-sized assemblages occurred mostly in tropical lowlands (figure 1a). The body size gradient of autochthon species resembled that of all species in both the Nearctic (r=0.672) and the Neotropics (r=0.651) (figure 1b). Nonetheless, differences were observed in the northernmost Nearctic and in the Amazonian lowlands, where mean body sizes were smaller for autochthon species (figure 1b). The presence of large-sized autochthons in Patagonia is also striking, suggesting Bergmann patterns for this species group in the coldest areas of the Neotropics (figure 1b; this is not a small-sample effect, as more than 25 autochthons inhabit the region – see Appendix 3).

The spatial body size patterns of GABI allochthons were virtually identical to the pattern of all species in the Neotropics (r=0.946) but were different in the Nearctic, where large mean body size values were uniformly distributed across the continent (figure 1c). This reflects that Nearctic assemblages of GABI allochthons comprise no more than five large species mostly inhabiting temperate, boreal and subarc-

(a) all species (b) autochthon species



(c) GABI allochthon species (d) eurasian allochthon species

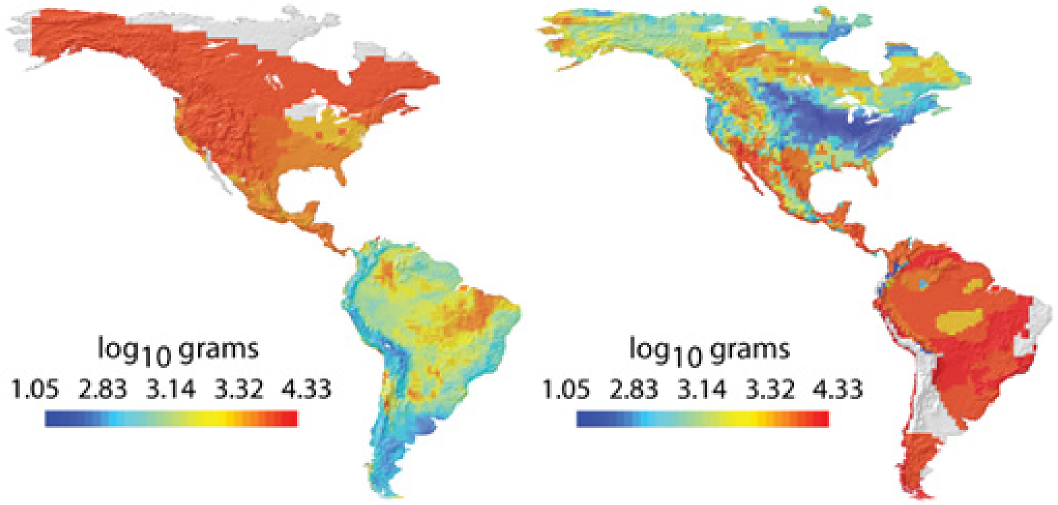


Figure 1. Geographical patterns of mean log10-body size for all species (a), autochthon species (b), GABI allochthon species (c) and Eurasian allochthon species in the New World. Maps of autochthons and allochthons were generated separately for North America and South America since autochthons species in one continent will be considered allochthon in the other.

tic latitudes (see Appendix 3). On the other hand, Eurasian allochthons showed a pattern of large-sized assemblages in Canada and along the Rocky Mountains (figure 1d). That pattern of large sizes in the North coincides with the latitudinal species richness gradient of Eurasian allochthons, which reverses the classical latitudinal species-richness gradient (see Appendix 3). Large-sized assemblages of Eurasian allochthons were also found throughout Central and South America (figure 1d), where a gradient of decreasing species-richness southwards is particularly evident – from the relatively poor Central America (with up to 7 species) to the highly-impoverished Patagonia (1 species) (see Appendix 3).

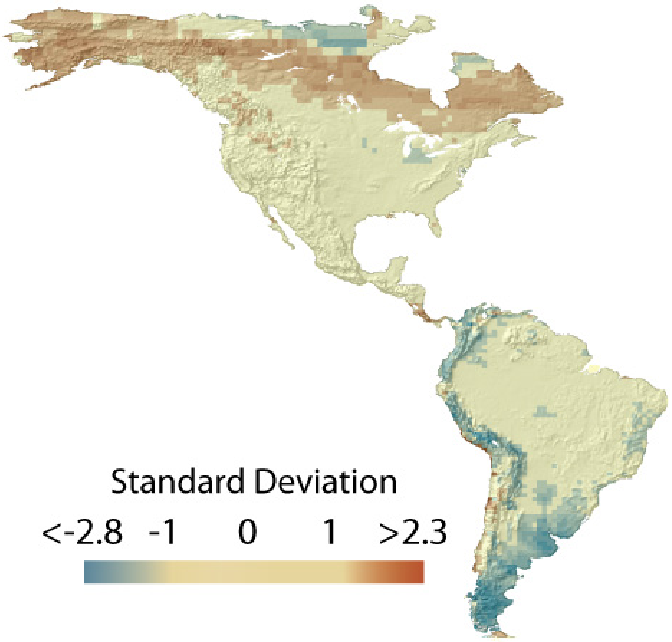


Figure 2. Standard Deviation of the difference between the body size patterns of all species and of autochthon species. Red colors indicate a positive contribution in body size due to allochthon clades. Blue colors indicate smaller sizes due to allochthons. While the presence of allochthons in the Nearctic influence the body size pattern with an increase in the average size of northernmost regions, it contributes with a decrease in size in southernmost regions of the Neotropics. A likely explanation for such reverse pattern must be related to the different nature of migrants to both subcontinents, and particularly in the radiation of small-sized rodents belonging to the family Muridae which are allochthons in the Neotropics.

In sum, Eurasian and GABI allochthons were differently distributed across the New World, and thus their participation in the body size gradient of all species differed among regions. Eurasian allochthons were more present in the Nearctic whereas GABI allochthons mostly influenced the body gradient in the Neotropics. Whereas Eurasian allochthons increased the mean body sizes of all species in the northernmost North America, and thus reinforced the region's Bergmannian latitudinal gradient (see above), GABI allochthons showed mean body sizes that were smaller than those of South American autochthons in Patagonia and the Andes, which had the reverse effect; that is, the GABI allochthons obscured the Bergmannian patterns found for autochthons in the Neotropics (figure 2).

Environmental correlates of mean body size

Our three-variable models accounted for over half the variation in mean body size of all species in both the Nearctic (R^2=0.546) and the Neotropics (R^2=0.503) (table 1). The inclusion in the models of spatial filters accounting for all residual spatial autocorrelation revealed meaningful amounts of spatially-structured variation that is unrelated with our environmental predictors, indicating that other spatially-structured factors or processes influence broad-scale body size gradients across the New World (Appendix 6). Also, the regression coefficients of OLS models were not affected by instability due to collinearity (all CN $\leq$ 3.127, VIF $\leq$ 2.625).

The Nearctic

Mean annual temperature was the primary predictor in all models except for Eurasian allochthons, which was the only group showing positive regression coefficients for temperature (table 1). However, the relationships of body size of all species and Eurasian allochthons with temperature were non-linear (Appendix 4). Lowess regression identified temperature thresholds where relationships with mammal body size shift from negative to positive (*ca.* 11ºC in both continents; see Rodríguez *et al.* 2008). Below the threshold, temperature became the main predictor for Eurasian allochthons body size as well, showing negative coefficients below the threshold and positive coefficients above it (Appendix 4).

Table 1. OLS environmental saturated models for mean log-10 body mass for all species, autochthon species and allochthon species from the GABI and Eurasia in both the Nearctic (a) and the Neotropics (b). Bold regression coefficients indicate the primary predictor in each model. Numbers of species included in each group are indicated (n). It is important to note that species considered autochthons in the Nearctic can be present as allochthons in the Neotropics and vice versa. Besides, the number of species belonging to genera that crossed to North America during the GABI which are currently present in the Nearctic is only a small proportion of all the species belonging to such genera (19 out of 113 species), and hence models for GABI allochthons in the Nearctic must be interpreted with caveats.

Region	Group	n	TEMP	NPP	RIE	R^2
Nearctic	All species	508	**-0.656**	-0.124	0.006	0.546
	Autochthons	429	**-0.338**	-0.120	-0.103	0.186
	Eurasian-allochthons	56	0.314	**-0.472**	0.191	0.211
	GABI-allochthons	19	**-0.455**	-0.419	0.061	0.619
Neotropics	All	669	**0.517**	0.004	-0.274	0.503
	Autochthons	322	0.054	0.094	**-0.395**	0.233
	GABI-allochthons	347	**0.785**	-0.147	0.051	0.425

Productivity was the secondary predictor in all models although it was the primary predictor for Eurasian allochthon body size when the whole range of temperatures was considered (table 1). Regression coefficients of productivity were negative in all cases (table 1) suggesting large mean body sizes in the less productive areas of the Nearctic. Range in elevation was the weakest predictor in all models of the Nearctic, with positive regression coefficients except for autochthons (table 1). However, it should be noted that the environmental model for autochthons was weaker than models for all species and both groups of allochthons, explaining less than a fifth of the variation in body size (table 1).

The Neotropics

Mean annual temperature was the main predictor in environmental models for body size of all species and GABI allochthons, showing positive standardized coefficients for those groups (table 1). As in the Nearctic, relationships of temperature with mean body size of all species and allochthons were non-linear (Appendix 4), with negative regression coefficients below an 11°C temperature threshold (Appendix 5). Unlike in the Nearctic, autochthon body size showed only a weak association with temperature and productivity, being more strongly linked with range in elevation (table 1). The negative coefficient of range in elevation indicates a trend of small autochthons in mountainous areas. In contrast, allochthon species body size was weakly but positively associated with range in elevation in the Neotropics (table 1). That association was stronger in cold areas of the Neotropics (i.e. below the 11°C threshold) where elevation became the primary predictor of allochthon body size, with a positive regression coefficient (Appendix 5). A positive association of allochthon body size with range in elevation was also observed in the Nearctic when temperature thresholds were taken into account (Appendix 5). As in the Nearctic, environmental models were stronger for all species and GABI allochthons than for autochthons in the Neotropics, where less than a quarter of the variation in autochthon body size was explained by the environmental predictors (table 1).

Table 1. Phylogenetic signal and phylogenetic autocorrelation metrics for mean log10-body size of all species, autochthons and allochthons as measured by Pagel's λ (1990), Blomgerg's K (Blomberg *et al.* 2003).

Group	*N*	Pagel's *λ*	LR *λ*	*p*≤	Blomberg's *K*	*p*≤
All species	1109	0.994	38.533	0.001	1.067	0.001
Autochthons	412	0.998	0.130	0.718	0.805	0.005
Allochthons	697	0.992	40.375	0.001	2.365	0.005

Phylogenetic autocorrelation in body size

Unsurprisingly, body size showed strong phylogenetic signal across all species and all subsets (table 2). Blomberg's K-statistic indicated stronger phylogenetic signal in body size than expected under BM for all species of the New World (K=1.067, p≤0.001) and for allochthons (K=2.308, p≤0.001). Phylogenetic signal for autochthon species was somewhat weaker than expected under BM (K=0.805, p≤0.005), although not significantly so according to the λ-statistic (table 2). These results suggest strong phylogenetic niche conservatism (PNC) (*sensu* Losos 2008) for body size of allochthons, but little PNC (*sensu* Losos 2008) for autochthon species. Interestingly, not only did autochthon body size have weaker PNC than allochthons or all species, but it also had weaker associations with the environmental variables (see table 1).

Phylogenetic autocorrelation patterns were very similar for all species and allochthon species across phylogenetic distances showing high Moran's *I* values up to150 Ma (Appendix 2). Autochthons had lower Moran's I values which decreased to levels near zero at 100 Ma (Appendix 2).

Discussion

The New World mammalian body size gradient is influenced by evolutionary and historical factors. Biotic exchanges during the Plio-Pleistocene period have left a detectable imprint in the mammal body size patterns of the Americas. Body size's relationships with phylogeny and environmental variables differ between autochthons and allochthons; the mixture of opposing signals configures the contemporary body size gradient of the New World mammals.

Support for ecological hypotheses also differed between the Nearctic and the Neotropics. Whereas the heat conservation hypothesis is favoured in the Nearctic, a positive association with temperature in combination with the habitat availability hypothesis emerges as the main statistical explanation for body size patterns in the Neotropics. Similar results were explained by Rodríguez *et al.* (2008) based solely on the specific environmental characteristics of each region (i.e. the Nearctic being colder in average than the Neotropics). When the nonlinearities in the correlations of body size with temperature are accounted for, the explanations for body size coincide in both the Nearctic and the Neotropics (Rodríguez *et al.* 2008; see Appendix 5).

The different evolutionary histories of the faunas of the two continents have also played a key role in determining the current body size gradient of New World mammals (*cf.* Rodríguez *et al.* 2008), in two main ways. First, assemblages are composed of authochthonous and allochthonous species, whose influences over the body size of all species patterns are different in the Nearctic and the Neotropics. Whereas the overall body size pattern in the Nearctic reflect the pattern seen in the autochthons, the overall pattern in the Neotropics is virtually identical to that for allochthons (see figure 1). This difference is probably due to the asymmetry of the GABI (Woodburne *et al.* 2006), with significantly more genera crossing from North to South (124 genera) than from South to North (16 genera). Likewise, the number of Eurasian genera arrived in North America (18 genera) differs from the few of those genera that reached South America (3 genera) (see Appendix 3). Furthermore, allochthons that moved into South America were particularly successful in colonizing the continent due to both competitive replacement (Webb 1976, 1985, Simpson 1980, but see Lessa & Fariña 1996) and Cenozoic climate changes with the subsequent niche conservatism dynamics (Webb 1991, Marquet & Cofré 1999).

Second, authochthon and allochthon species show different associations between body size and environmental predictors (see table 1). Autochthons show weaker associations and hence less pronounced spatial gradients in body size than allochthons. Autochthon size is mainly associated with temperature in the Nearctic, but only weakly related to temperature and productivity in the Neotropics. In contrast, allochthon body size shows a nonlinear relationship with temperature and a positive relationship with range in elevation in both the Nearctic and the Neotropics. These results suggest an influence of the time that clades have had available to adapt and diversify.

The strong phylogenetic signal in mammalian body size is not a novel finding (e.g., Freckleton *et al.* 2002, Cooper & Purvis 2010), but the stronger signal in allochthons than autochtons is. While the evolution of body size in autochthons appears compatible with BM, allochthon body sizes are more similar among closely related species than expected under BM (table 2), suggesting PNC *sensu* Losos (2008) for the latter group. This does not mean that size has evolved more slowly in allochthons than in autochthons; rather, it might indicate that allochthons have had less time to occupy a broader range of the niche space (i.e., diversifying body sizes). Besides, the strong phylogenetic signal in allochthon body size might partly reflect that clades that have participated in biotic exchanges are those with strong dispersal abilities. It is possible that dispersal ability, which is associated with body size (Wolff 1999, Sutherland *et al.* 2000, Bowman *et al.* 2002), is the phylogenetically conserved trait instead of body size, although we cannot not explicitly test that supposition.

Differences between autochthon and allochthon species in body size's phylogenetic signal and in its environmental correlates can be interpreted in terms of a straightforward mechanism. Hortal *et al.* (2011) formally demonstrated that more climatically stable areas promoted diversification and occupation of the niche space in European dung beetles during the Pleistocene, whereas in areas that suffered from strong climatic shifts (i.e. glaciations) macroclimate and niche conservatistm acted as filters limiting the number of species able to disperse to those areas and constraining where each one could survive. Similarly, we hypothesize that climatic stability would produce an equivalent effect on the amount of time available to each group to diversify. That is, assuming that autochthon clades have been present in either North America or South America for longer than allochthon clades, they have had more time to diversify and occupy a wider range of niche space, as predicted by the time-for-speciation effect (e.g., Stephens and Wiens 2003). In contrast, allochthons, which have colonised and diversified more recently, would be composed of mostly large-sized clades that are able to participate in long distance migrations due to higher dispersal abilities (e.g. Wolff 1999, Sutherland *et al.* 2000, Bowman *et al.* 2002). Arriving allochthons would not distribute uniformly across the continents, but rather remain in the most suitable habitats due to niche conservatism (Peterson et al 1999, Wiens & Donoghue 2005). Allochthons similarly to post-glacial dispersers would be conditioned by climatic filtering and previous adaptations (to climates in biogeographic regions where the groups originated), thus showing a tendency to reproduce existing climatic gradients. Allochthon clades, filtered by macroclimate and selected by their dispersal abilities, would encompass a subset of species showing higher phylogenetic signal for body size than autochthons.

An additional support for this mechanism is provided by the different biogeographic origin of allochthon species in North and South America. Allochthons colonizing the Nearctic from Eurasia since the late Pliocene were adapted to cold and temperate climates (Webb & Barnosky 1989) that were similar to the environments preferred by the largest autochthon species. In contrast, mammal genera participating in the GABI and migrating to South America would have been adapted to warm open savanna settings prior to migration (Webb & Rancy 1996). Furthermore, richness patterns of allochthons show how species belonging to genera coming from Eurasia would have progressively colonized the Nearctic with only few reaching the far south (see Appendix 3). The same colonization pattern is shown by GABI allochthons not being able to reach the northern Nearctic and by fewer species reaching the southernmost regions of South America (see Appendix 3).

The large-bodied assemblages of autochthon species in southernmost South America (see figure 1b) are an intriguing finding. Such a Bergmann-like pattern is not found in mammals overall (Rodríguez *et al.* 2008) or within the carnivores (Diniz-Filho *et al.* 2009), although it has been found for birds (Rameriz *et al.* 2008). The reason for the lack of a trend in the whole set of species could the presence of small-sized allochthon clades in South America. This is one of the most obvious effects of allochthon clades on the body size patterns of mammals in the New World. Whereas the average of body size increases – by over 1 standard deviation – in northernmost regions of the Nearctic, it decreases in cold regions of southernmost Neotropics due to the presence of allochthons (figure 2). An example of taxa potentially responsible for this is the sigmodontine rodents, which had radiated in the Miocene of North America (Baskin 1986). This clade would have found suitable habitats in the coldest southernmost Neotropics formerly inhabited by larger autochthon species and might have induced a subsequent decrease in average body size in such regions (see figure 2).

Finally, we acknowledge that the spatial variation in mammal body size is sure to also reflect other macroevolutionary processes such as different centres of diversification, or spatial gradients in speciation and extinction rates. The spatial variation in body size that is unrelated to our environmental variables might be explained by such factors although measuring them is difficult. Also, differential extinctions – known to have affected primarily large species (e.g., Martin & Steadman 1999) – could have played a role in determining body size patterns, especially for South America that underwent the largest Late Pleistocene megamammal extinction event (Cione *et al.* 2009). Comprehensive data on centres of diversification and mammalian extinctions will provide a more complete picture of the influence of evolutionary history on contemporary patterns. For the time being, this work provides evidence of how late Cenozoic biotic exchanges have helped to configure the body size gradients of New World mammals.

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Supporting Information

Additional Supporting Information may be found in:

Appendix 1. New World mammal species checklist.

Appendix 2. Moran's I phylogenetic correlograms.

Appendix 3. Species richness geographical patterns.

Appendix 4. Non-linearities in mean log10-body mass vs. temperature.

Appendix 5. OLS environmental models below and above temperature threshold.

Appendix 6. OLS environmental models including spatial variation independent from the spatial structure in body mass explained by environmental predictors.

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Appendix 1

New World mammal species checklist indicating their body masses in grams between parentheses. Species belonging to genera involved in biotic exchanges are indicated either if they belong to genera arrived to the Americas from Eurasia (^{eu}), or to genera involved in the GABI arriving to North America (^{gn}) or to South America (^{gs})

Abrawayaomys ruschii (63.0)^{gs}, *Abrocoma bennettii* (250.5), *A. boliviensis* (158.0), *A. cinerea* (250.0), *Aconaemys fuscus* (133.5), *A. sagei* (96.5), *Aepeomys fuscatus* (49.5)^{gs}, *A. lugens* (37.0)^{gs}, *Agouti paca* (8000.0), *A. taczanowskii* (8999.9), *Akodon aerosus* (60.0)^{gs}, *A. affinis* (24.9)^{gs}, *A. albiventer* (21.8)^{gs}, *A. azarae* (25.0)^{gs}, *A. bogotensis* (13.0)^{gs}, *A. boliviensis* (27.5)^{gs}, *A. budini* (26.9)^{gs}, *A. cursor* (39.9)^{gs}, *A. dayi* (32.5)^{gs}, *A. dolores* (50.5)^{gs}, *A. fumeus* (22.7)^{gs}, *A. hershkovitzi* (21.3)^{gs}, *A. illuteus* (47.8)^{gs}, *A. iniscatus* (28.7)^{gs}, *A. juninensis* (39.0)^{gs}, *A. kempi* (26.4)^{gs}, *A. kofordi* (29.5)^{gs}, *A. lanosus* (32.5)^{gs}, *A. latebricola* (39.0)^{gs}, *A. lindberghi* (26.4)^{gs}, *A. longipilis* (37.6)^{gs}, *A. mimus* (24.0)^{gs}, *A. molinae* (33.0)^{gs}, *A. mollis* (30.4)^{gs}, *A. neocenus* (42.4)^{gs}, *A. nigrita* (19.9)^{gs}, *A. olivaceus* (27.0)^{gs}, *A. orophilus* (39.0)^{gs}, *A. puer* (20.7)^{gs}, *A. sanborni* (24.7)^{gs}, *A. sanctipaulensis* (27.1)^{gs}, *A. serrensis* (28.3)^{gs}, *A. siberiae* (34.6)^{gs}, *A. simulator* (42.5)^{gs}, *A. spegazzinii* (28.6)^{gs}, *A. subfuscus* (30.4)^{gs}, *A. surdus* (39.0)^{gs}, *A. sylvanus* (39.0)^{gs}, *A. toba* (51.2)^{gs}, *A. torques* (39.0)^{gs}, *A. varius* (40.0)^{gs}, *Alces alces* (358996.3)^{eu}, *Alopex lagopus* (3450.0), *Alouatta belzebul* (6400.0)^{gn}, *A. caraya* (5862.5)^{gn}, *A. palliata* (7274.9)^{gn}, *A. pigra* (7000.0)^{gn}, *A. sara* (6611.0)^{gn}, *A. seniculus* (6145.5)^{gn}, *Ammospermophilus harrisii* (122.0), *A. interpres* (110.3), *A. leucurus* (103.7), *A. nelsoni* (160.4), *Andalgalomys olrogi* (32.9)^{gs}, *A. pearsoni* (25.4)^{gs}, *Andinomys edax* (69.7)^{gs}, *Anotomys leander* (66.4)^{gs}, *Antilocapra americana* (46082.9), *Aotus azarai* (962.9)^{gn}, *A. lemurinus* (873.0)^{gn}, *A. miconax* (800.0)^{gn}, *A. nancymaae* (788.0)^{gn}, *A. nigriceps* (1060.0)^{gn}, *A. trivirgatus* (900.0)^{gn}, *A. vociferans* (873.0)^{gn}, *Aplodontia rufa* (1004.0), *Arborimus albipes* (23.0)^{gs}, *A. longicaudus* (21.8)^{gs}, *A. pomo* (32.5)^{gs}, *Ateles belzebuth* (5000.0)^{gn}, *A. chamek* (6000.0)^{gn}, *A. fusciceps* (9100.0)^{gn}, *A. geoffroyi* (5284.9)^{gn}, *A. marginatus* (6000.0)^{gn}, *A. paniscus* (7900.1)^{gn}, *Atelocynus microtis* (7750.0)^{gs}, *Auliscomys boliviensis* (65.7)^{gs}, *A. micropus* (72.7)^{gs}, *A. pictus* (54.7)^{gs}, *A. sublimis* (38.0)^{gs}, *Baiomys musculus* (9.0)^{gs}, *B. taylori* (8.0)^{gs}, *Bassaricyon alleni* (1235.0)^{gs}, *B. beddardi* (1235.0)^{gs}, *B. gabbii* (1250.0)^{gs}, *B. lasius* (1200.0)^{gs}, *B. pauli* (1200.0)^{gs}, *Bassariscus astutus* (1129.5), *B. sumichrasti* (900.0), *Bibimys chacoensis* (28.0)^{gs}, *B. labiosus* (28.0)^{gs}, *B. torresi* (28.0)^{gs}, *Blarina brevicauda* (28.0), *B. carolinensis* (13.5), *B. hylophaga* (14.5), *Blarinomys breviceps* (36.8)^{gs}, *Blastocerus dichotomus* (86666.2)^{gs}, *Bolomys amoenus* (29.0)^{gs}, *B. lactens* (32.9)^{gs}, *B. lasiurus* (39.9)^{gs}, *B. obscurus* (40.7)^{gs}, *B. punctulatus* (37.3)^{gs}, *B. temchuki* (47.2)^{gs}, *Brachylagus idahoensis* (421.3), *Brachyteles arachnoides* (13499.9)^{gn}, *Bradypus torquatus* (3900.0)^{gn}, *B. tridactylus* (3850.0)^{gn}, *B. variegatus* (4335.0)^{gn}, *Cabassous centralis* (3810.0)^{gn}, *C. chacoensis* (1490.0)^{gn}, *C. tatouay* (5350.0)^{gn}, *C. unicinctus* (4800.0)^{gn}, *Cacajao calvus* (5796.0)^{gn}, *C. melanocephalus* (3800.0)^{gn}, *Caenolestes caniventer* (40.0), *C. convelatus* (40.0), *C. fuliginosus* (27.8), *Callicebus brunneus* (992.4)^{gn}, *C. caligatus* (992.4)^{gn}, *C. cinerascens* (992.4)^{gn}, *C. cupreus* (915.0)^{gn}, *C. donacophilus* (795.0)^{gn}, *C. dubius* (992.4)^{gn}, *C. hoffmannsi* (992.4)^{gn}, *C. modestus* (992.4)^{gn}, *C. moloch* (854.7)^{gn}, *C. oenanthe* (992.4)^{gn}, *C. olallae* (992.4)^{gn}, *C. personatus* (1350.0)^{gn}, *C. torquatus* (1050.0)^{gn}, *Callimico goeldii* (480.0)^{gn}, *Callithrix argentata* (440.0)^{gn}, *C. aurita* (342.0)^{gn}, *C. flaviceps* (342.0)^{gn}, *C. geoffroyi* (342.0)^{gn}, *C. humeralifera* (350.0)^{gn}, *C. jacchus* (292.0)^{gn}, *C. kuhlii* (342.0)^{gn}, *C. penicillata* (342.0)^{gn}, *C. pygmaea* (125.0)^{gn}, *Calomys boliviae* (27.0)^{gs}, *C. callidus* (27.0)^{gs}, *C. callosus* (45.0)^{gs}, *C. hummelincki* (27.0)^{gs}, *C. laucha* (14.0)^{gs}, *C. lepidus* (26.6)^{gs}, *C. musculinus* (20.1)^{gs}, *C. sorellus* (20.0)^{gs}, *C. tener* (13.8)^{gs}, *Caluromys derbianus* (297.0), *C. lanatus* (325.0), *C. philander* (229.3), *Caluromysiops irrupta* (250.0), *Canis latrans* (13406.3)^{eu}, *C. lupus* (42750.0)^{eu}, *Carterodon sulcidens* (113.8), *Castor canadensis* (21820.0), *Catagonus wagneri* (35566.4)^{gs}, *Cavia aperea* (549.0), *C. fulgida* (282.5), *C. magna* (460.0), *C. tschudii* (1000.0), *Cebus albifrons* (2629.0)^{gn}, *C. apella* (2500.0)^{gn}, *C. capucinus* (2733.3)^{gn}, *C. olivaceus* (2600.0)^{gn}, *Cerdocyon thous* (5240.0)^{gs}, *Cervus elaphus* (217750.9)^{eu}, *Chaetodipus arenarius* (23.0), *C. artus* (20.6), *C. baileyi* (26.3), *C. californicus* (22.0), *C. fallax* (18.7), *C. formosus* (19.5), *C. goldmani* (23.0), *C. hispidus* (32.0), *C. intermedius* (16.5), *C. lineatus* (23.0), *C. nelsoni* (15.7), *C. penicillatus* (15.0), *C. pernix* (17.0), *C. spinatus* (16.4), *Chaetomys subspinosus* (1300.0), *Chaetophractus nationi* (2150.0), *C. vellerosus* (1030.0), *C. villosus* (4540.0), *Chelemys macronyx* (73.3)^{gs}, *C. megalonyx* (50.8)^{gs}, *Chibchanomys trichotis* (50.0)^{gs}, *Chilomys instans* (19.0)^{gs}, *Chinchilla brevicaudata* (500.0), *C. lanigera* (485.0), *Chinchillula sahamae* (169.8)^{gs}, *Chironectes minimus* (946.0), *Chiropotes albinasus* (2900.0)^{gn}, *C. satanas* (3000.0)^{gn}, *Chlamyphorus retusus* (130.0), *C. truncatus* (44.3), *Choloepus didactylus* (5160.0)^{gn}, *C. hoffmanni* (6000.0)^{gn}, *Chroeomys andinus* (18.0)^{gs}, *C. jelskii* (34.5)^{gs}, *Chrysocyon brachyurus* (23249.8)^{gs}, *Clethrionomys californicus* (18.3)^{eu}, *C. gapperi* (19.0)^{eu}, *C. rutilus* (29.0)^{eu}, *Clyomys bishopi* (30.0), *C. laticeps* (201.0), *Coendou bicolor* (4050.0)^{gn}, *C. koopmani* (3000.0)^{gn}, *C. prehensilis* (4400.0)^{gn}, *C. rothschildi* (2000.0)^{gn}, *Condylura cristata* (84.0), *Conepatus chinga* (1917.5)^{gs}, *C. humboldtii* (328.0)^{gs}, *C. leuconotus* (3500.0)^{gs}, *C. semistriatus* (1200.0)^{gs}, *Cryptotis endersi* (7.0)^{gs}, *C. goldmani* (8.0)^{gs}, *C. goodwini* (7.0)^{gs}, *C. gracilis* (7.0)^{gs}, *C. hondurensis* (7.0)^{gs}, *C. magna* (7.0)^{gs}, *C. meridensis* (12.0)^{gs}, *C. mexicana* (7.0)^{gs}, *C. montivaga* (11.3)^{gs}, *C. nigrescens* (7.0)^{gs}, *C. parva* (5.0)^{gs}, *C. squamipes* (11.0)^{gs}, *C. thomasi* (12.6)^{gs}, *Ctenomys argentinus* (221.3), *C. australis* (361.5), *C. azarae* (400.0), *C. boliviensis* (535.0), *C. bonettoi* (202.3), *C. brasiliensis* (400.0), *C. colburni* (400.0), *C. conoveri* (860.0), *C. dorsalis* (165.6), *C. emilianus* (285.3), *C. frater* (172.9), *C. fulvus* (262.0), *C. haigi* (164.0), *C. knighti* (316.0), *C. latro* (192.0), *C. leucodon* (243.6), *C. lewisi* (117.2), *C. magellanicus* (272.0), *C. maulinus* (215.0), *C. mendocinus* (177.5), *C. minutus* (92.0), *C. occultus* (150.0), *C. opimus* (361.5), *C. pearsoni* (212.0), *C. perrensis* (400.0), *C. peruanus* (490.0), *C. pontifex* (400.0), *C. porteousi* (192.4), *C. saltarius* (230.0), *C. sericeus* (400.0), *C. sociabilis* (400.0), *C. steinbachi* (385.0), *C. talarum* (132.3), *C. torquatus* (209.5), *C. tuconax* (249.0), *C. tucumanus* (217.0), *C. validus* (232.6), *Cyclopes didactylus* (329.5)^{gn}, *Cynomys gunnisoni* (925.0), *C. leucurus* (908.5), *C. ludovicianus* (1364.0), *C. mexicanus* (900.0), *C. parvidens* (900.0), *Dactylomys boliviensis* (728.8), *D. dactylinus* (650.0), *D. peruanus* (382.0), *Dasyprocta azarae* (2310.0), *D. fuliginosa* (3500.0), *D. guamara* (2650.0), *D. kalinowskii* (2650.0), *D. leporina* (3020.0), *D. mexicana* (5000.0), *D. prymnolopha* (2900.0), *D. punctata* (2675.0), *Dasypus hybridus* (1500.0)^{gn}, *D. kappleri* (9500.0)^{gn}, *D. novemcinctus* (4203.8)^{gn}, *D. pilosus* (4445.0)^{gn}, *D. sabanicola* (1150.0)^{gn}, *D. septemcinctus* (1526.7)^{gn}, *Delomys dorsalis* (67.5)^{gs}, *D. sublineatus* (90.0)^{gs}, *Dicrostonyx groenlandicus* (54.4)^{eu}, *D. hudsonius* (57.0)^{eu}, *D. nunatakensis* (54.4)^{eu}, *D. richardsoni* (54.4)^{eu}, *Didelphis albiventris* (904.0)^{gn}, *D. aurita* (1164.0)^{gn}, *D. marsupialis* (1091.2)^{gn}, *D. virginiana* (2195.5)^{gn}, *Dinomys branickii* (12500.0), *Diplomys caniceps* (394.5), *D. labilis* (227.5), *D. rufodorsalis* (144.8), *Dipodomys agilis* (57.8), *D. californicus* (72.0), *D. compactus* (60.4), *D. deserti* (104.5), *D. elator* (77.5), *D. gravipes* (84.0), *D. heermanni* (72.0), *D. ingens* (133.9), *D. merriami* (42.0), *D. microps* (54.6), *D. nelsoni* (88.6), *D. nitratoides* (43.9), *D. ordii* (60.4), *D. panamintinus* (74.7), *D. phillipsii* (41.0), *D. spectabilis* (135.9), *D. stephensi* (69.8), *D. venustus* (72.0), *Dolichotis patagonum* (8000.0), *D. salinicola* (1600.0), *Dromiciops gliroides* (22.3), *Echimys blainvillei* (243.3), *E. braziliensis* (312.5), *E. chrysurus* (652.5), *E. dasythrix* (260.0), *E. grandis* (584.0), *E. lamarum* (215.2), *E. macrurus* (439.0), *E. nigrispinus* (224.3), *E. pictus* (519.0), *E. rhipidurus* (315.0), *E. saturnus* (626.9), *E. semivillosus* (200.0), *E. thomasi* (560.2), *Echinoprocta rufescens* (831.8), *Eira barbara* (3910.0)^{gs}, *Eligmodontia moreni* (18.0)^{gs}, *E. morgani* (16.5)^{gs}, *E. puerulus* (28.5)^{gs}, *E. typus* (17.3)^{gs}, *Erethizon dorsatum* (7085.3)^{gn}, *Euneomys chinchilloides* (87.6)^{gs}, *E. fossor* (83.0)^{gs}, *E. mordax* (82.0)^{gs}, *E. petersoni* (83.0)^{gs}, *Euphractus sexcinctus* (4782.9), *Euryzygomatomys spinosus* (187.5), *Galea flavidens* (450.0), *G. musteloides* (480.0), *G. spixii* (326.2), *Galenomys garleppi* (59.3)^{gs}, *Galictis cuja* (1000.0)^{gs}, *G. vittata* (3200.0)^{gs}, *Geomys arenarius* (206.0), *G. bursarius* (203.8), *G. personatus* (397.0), *G. pinetis* (85.0), *G. tropicalis* (350.0), *Geoxus valdivianus* (31.5)^{gs}, *Glaucomys sabrinus* (166.0), *G. volans* (63.9), *Gracilinanus aceramarcae* (20.5), *G. agilis* (22.0), *G. dryas* (18.0), *G. emiliae* (7.6), *G. marica* (23.8), *G. microtarsus* (31.0), *Graomys domorum* (102.0)^{gs}, *G. edithae* (40.4)^{gs}, *G. griseoflavus* (67.5)^{gs}, *Gulo gulo* (14525.1)^{eu}, *Habromys chinanteco* (40.0)^{gs}, *H. lepturus* (85.0)^{gs}, *H. lophurus* (40.0)^{gs}, *H. simulatus* (40.0)^{gs}, *Herpailurus yaguarondi* (8999.9)^{gs}, *Heteromys anomalus* (70.0)^{gs}, *H. australis* (267.5)^{gs}, *H. desmarestianus* (72.5)^{gs}, *H. gaumeri* (63.6)^{gs}, *H. nelsoni* (54.2)^{gs}, *H. oresterus* (74.8)^{gs}, *Hippocamelus antisensis* (68599.3)^{gs}, *H. bisulcus* (70000.3)^{gs}, *Hodomys alleni* (367.6)^{gs}, *Holochilus brasiliensis* (155.0)^{gs}, *H. chacarius* (204.0)^{gs}, *H. magnus* (238.5)^{gs}, *H. sciureus* (163.5)^{gs}, *Hoplomys gymnurus* (240.0), *Hydrochaeris hydrochaeris* (62449.6)^{gn}, *Ichthyomys hydrobates* (66.4)^{gs}, *I. pittieri* (69.1)^{gs}, *I. stolzmanni* (84.7)^{gs}, *I. tweedii* (118.5)^{gs}, *Irenomys tarsalis* (43.1)^{gs}, *Isothrix bistriata* (445.0), *I. pagurus* (210.0), *Isthmomys flavidus* (138.0)^{gs}, *I. pirrensis* (138.0)^{gs}, *Kannabateomys amblyonyx* (600.0), *Kerodon rupestris* (800.0), *Kunsia fronto* (168.0)^{gs}, *K. tomentosus* (115.6)^{gs}, *Lagidium peruanum* (1220.0), *L. viscacia* (1540.0), *L. wolffsohni* (2682.0), *Lagostomus maximus* (4647.5), *Lagothrix flavicauda* (6800.0)^{gn}, *L. lagotricha* (6300.0)^{gn}, *Lama guanicoe* (120000.0)^{gs}, *Lemmiscus curta-*

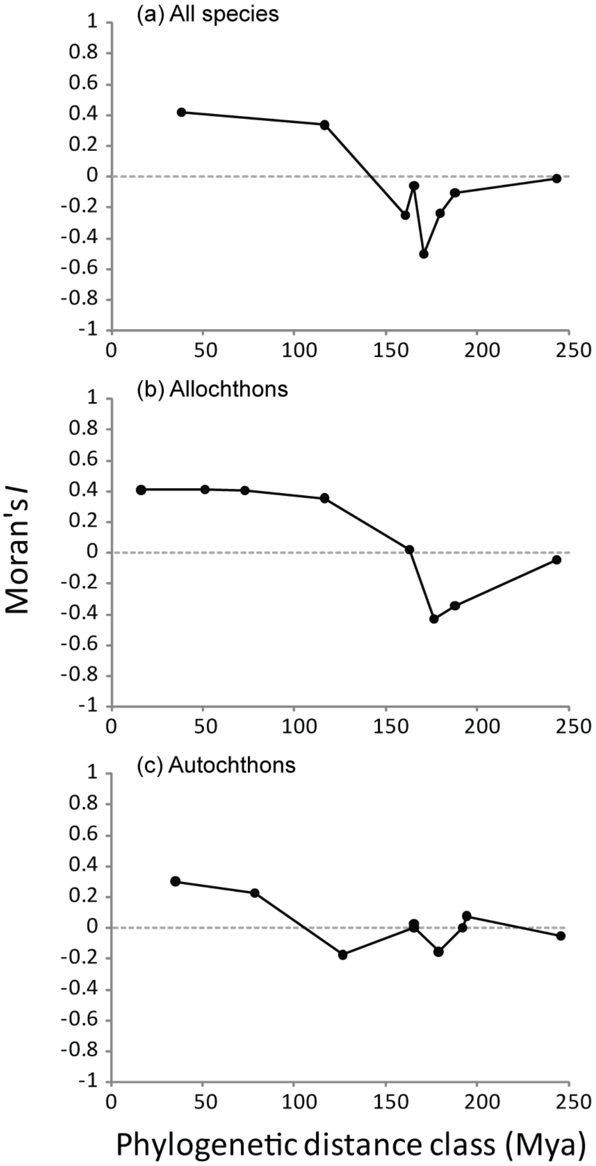
tus (28.3)^{gs}, *Lemmus sibiricus* (52.3)^{eu}, *Lenoxus apicalis* (53.6)^{gs}, *Leontopithecus caissara* (535.5)^{gn}, *L. chrysomelas* (700.0)^{gn}, *L. chrysopygus* (700.0)^{gn}, *L. rosalia* (535.5)^{gn}, *Leopardus pardalis* (11900.1)^{gs}, *L. tigrinus* (2250.0)^{gs}, *L. wiedii* (3250.0)^{gs}, *Lepus alleni* (3685.0)^{eu}, *L. americanus* (1710.0)^{eu}, *L. arcticus* (4405.0)^{eu}, *L. californicus* (2422.5)^{eu}, *L. callotis* (2500.0)^{eu}, *L. flavigularis* (3000.0)^{eu}, *L. othus* (4806.0)^{eu}, *L. townsendii* (1555.0)^{eu}, *Lestodelphys halli* (76.0), *Lestoros inca* (21.1), *Liomys adspersus* (65.0), *L. irroratus* (50.0), *L. pictus* (40.0), *L. salvini* (42.0), *L. spectabilis* (65.0), *Lonchothrix emiliae* (138.2), *Lontra canadensis* (8087.4)^{eu}, *L. felina* (30600.0)^{eu}, *L. longicaudis* (6555.0)^{eu}, *L. provocax* (7500.0)^{eu}, *Lutreolina crassicaudata* (537.3), *Lyncodon patagonicus* (225.0)^{gs}, *Lynx canadensis* (9373.2)^{eu}, *L. rufus* (8904.1)^{eu}, *Makalata armata* (108.0), *Marmosa andersoni* (47.4), *M. canescens* (60.0), *M. lepida* (14.0), *M. mexicana* (49.5), *M. murina* (26.0), *M. robinsoni* (56.7), *M. rubra* (63.0), *M. tyleriana* (32.4), *M. xerophila* (46.2), *Marmosops cracens* (25.5), *M. fuscatus* (60.0), *M. handleyi* (30.7), *M. impavidus* (40.5), *M. incanus* (62.3), *M. invictus* (29.2), *M. noctivagus* (21.0), *M. parvidens* (15.0), *Marmota broweri* (3600.0), *M. caligata* (7230.0), *M. flaviventris* (3350.0), *M. monax* (3801.7), *M. olympus* (6300.0), *Martes americana* (1250.0), *M. pennanti* (4000.0), *Mazama americana* (22799.7)^{gs}, *M. bricenii* (16499.9)^{gs}, *M. chunyi* (16499.9)^{gs}, *M. gouazoupira* (16300.1)^{gs}, *M. nana* (16499.9)^{gs}, *M. rufina* (25999.8)^{gs}, *Megadontomys cryophilus* (32.0)^{gs}, *M. nelsoni* (111.0)^{gs}, *M. thomasi* (111.0)^{gs}, *Megasorex gigas* (20.0), *Melanomys caliginosus* (41.0)^{gs}, *M. robustulus* (53.5)^{gs}, *M. zunigae* (53.5)^{gs}, *Mephitis macroura* (801.3), *M. mephitis* (2085.0), *Mesomys hispidus* (175.0), *M. leniceps* (108.0), *M. stimulax* (108.0), *Metachirus nudicaudatus* (375.0), *Micoureus alstoni* (132.3), *M. constantiae* (90.0), *M. demerarae* (75.8), *M. regina* (118.6), *Microcavia australis* (286.1), *M. niata* (255.2), *M. shiptoni* (185.0), *Microdipodops megacephalus* (10.5), *M. pallidus* (12.5), *Microryzomys altissimus* (13.5)^{gs}, *M. minutus* (13.5)^{gs}, *Microsciurus alfari* (87.5)^{gs}, *M. flaviventer* (92.0)^{gs}, *M. mimulus* (120.0)^{gs}, *M. santanderensis* (99.8)^{gs}, *Microtus californicus* (57.4)^{eu}, *M. canicaudus* (28.4)^{eu}, *M. chrotorrhinus* (39.0)^{eu}, *M. guatemalensis* (42.0)^{eu}, *M. longicaudus* (46.7)^{eu}, *M. mexicanus* (35.0)^{eu}, *M. miurus* (41.0)^{eu}, *M. montanus* (36.3)^{eu}, *M. oaxacensis* (39.2)^{eu}, *M. ochrogaster* (38.0)^{eu}, *M. oeconomus* (32.2)^{eu}, *M. oregoni* (20.3)^{eu}, *M. pennsylvanicus* (36.8)^{eu}, *M. pinetorum* (26.3)^{eu}, *M. quasiater* (40.0)^{eu}, *M. richardsoni* (85.0)^{eu}, *M. townsendii* (64.8)^{eu}, *M. umbrosus* (42.0)^{eu}, *M. xanthognathus* (125.8)^{eu}, *Monodelphis adusta* (35.0), *M. americana* (19.5), *M. brevicaudata* (69.6), *M. dimidiata* (58.0), *M. domestica* (71.4), *M. emiliae* (40.0), *M. iheringi* (112.0), *M. kunsi* (11.3), *M. maraxina* (109.3), *M. osgoodi* (112.0), *M. rubida* (45.5), *M. scalops* (741.0), *M. sorex* (48.0), *M. theresa* (112.0), *M. unistriata* (55.3), *Mustela africana* (537.0)^{eu}, *M. erminea* (70.0)^{eu}, *M. felipei* (211.3)^{eu}, *M. frenata* (147.0)^{eu}, *M. nivalis* (46.9)^{eu}, *M. vison* (945.0)^{eu}, *Myocastor coypus* (6937.5), *Myoprocta acouchy* (600.0), *Myrmecophaga tridactyla* (22333.2)^{gn}, *Napaeozapus insignis* (22.3), *Nasua narica* (4030.0)^{gs}, *N. nasua* (3793.8)^{gs}, *Nasuella olivacea* (1340.0)^{gs}, *Neacomys guianae* (14.2)^{gs}, *N. pictus* (19.0)^{gs}, *N. spinosus* (19.0)^{gs}, *N. tenuipes* (19.0)^{gs}, *Nectomys palmipes* (190.7)^{gs}, *N. parvipes* (248.8)^{gs}, *N. squamipes* (190.7)^{gs}, *Nelsonia goldmani* (28.5)^{gs}, *N. neotomodon* (80.0)^{gs}, *Neofiber alleni* (266.0)^{gs}, *Neotoma albigula* (206.0)^{gs}, *N. angustapalata* (198.0)^{gs}, *N. chrysomelas* (203.0)^{gs}, *N. cinerea* (299.2)^{gs}, *N. devia* (200.0)^{gs}, *N. floridana* (244.7)^{gs}, *N. fuscipes* (229.8)^{gs}, *N. goldmani* (198.0)^{gs}, *N. lepida* (163.7)^{gs}, *N. mexicana* (203.0)^{gs}, *N. micropus* (237.5)^{gs}, *N. nelsoni* (198.0)^{gs}, *N. palatina* (198.0)^{gs}, *N. phenax* (227.5)^{gs}, *N. stephensi* (152.5)^{gs}, *Neotomodon alstoni* (40.0)^{gs}, *Neotomys ebriosus* (64.5)^{gs}, *Neurotrichus gibbsii* (8.9), *Neusticomys monticolus* (39.5)^{gs}, *N. mussoi* (40.0)^{gs}, *N. oyapocki* (4.7)^{gs}, *N. peruviensis* (40.0)^{gs}, *N. venezuelae* (47.1)^{gs}, *Notiomys edwardsii* (21.3)^{gs}, *Notiosorex crawfordi* (4.4), *Nyctomys sumichrasti* (60.0)^{gs}, *Ochotona collaris* (129.0), *O. princeps* (157.6), *Ochrotomys nuttalli* (22.4)^{gs}, *Octodon bridgesi* (150.0), *O. degus* (210.0), *O. lunatus* (233.0), *Octodontomys gliroides* (150.0), *Octomys mimax* (131.0), *Odocoileus hemionus* (54212.6)^{gs}, *O. virginianus* (55508.6)^{gs}, *Oecomys bicolor* (34.0)^{gs}, *O. cleberi* (73.4)^{gs}, *O. concolor* (61.6)^{gs}, *O. flavicans* (73.4)^{gs}, *O. mamorae* (62.5)^{gs}, *O. paricola* (73.4)^{gs}, *O. phaeotis* (73.4)^{gs}, *O. rex* (73.4)^{gs}, *O. roberti* (73.4)^{gs}, *O. rutilus* (73.4)^{gs}, *O. speciosus* (73.4)^{gs}, *O. superans* (73.4)^{gs}, *O. trinitatis* (73.4)^{gs}, *Olallamys albicauda* (273.5), *O. edax* (206.4), *Oligoryzomys andinus* (25.2)^{gs}, *O. arenalis* (25.2)^{gs}, *O. chacoensis* (23.0)^{gs}, *O. delticola* (29.4)^{gs}, *O. destructor* (25.2)^{gs}, *O. eliurus* (30.0)^{gs}, *O. flavescens* (21.3)^{gs}, *O. fulvescens* (25.0)^{gs}, *O. griseolus* (25.2)^{gs}, *O. longicaudatus* (27.0)^{gs}, *O. magellanicus* (25.2)^{gs}, *O. microtis* (22.5)^{gs}, *O. nigripes* (20.5)^{gs}, *O. vegetus* (25.0)^{gs}, *Oncifelis colocolo* (3935.0)^{gs}, *O. geoffroyi* (3590.0)^{gs}, *O. guigna* (2230.0)^{gs}, *Ondatra zibethicus* (981.5)^{gs}, *Onychomys arenicola* (30.0)^{gs}, *O. leucogaster* (27.9)^{gs}, *O. torridus* (25.0)^{gs}, *Oreailurus jacobita* (9170.0), *Oreamnos americanus* (72500.3), *Orthogeomys cavator* (650.0)^{gs}, *O. cherriei* (615.0)^{gs}, *O. cuniculus* (500.0)^{gs}, *O. dariensis* (438.0)^{gs}, *O. grandis* (500.0)^{gs}, *O. heterodus* (615.0)^{gs}, *O. hispidus* (500.0)^{gs}, *O. lanius* (500.0)^{gs}, *O. matagalpae* (494.1)^{gs}, *O. thaeleri* (438.0)^{gs}, *O. underwoodi* (250.0)^{gs}, *Oryzomys albigularis* (60.5)^{gs}, *O. alfaroi* (33.3)^{gs}, *O.*

auriventer (60.5)^{gs}, *O. balneator* (60.5)^{gs}, *O. bolivaris* (60.5)^{gs}, *O. buccinatus* (144.0)^{gs}, *O. capito* (57.8)^{gs}, *O. chapmani* (50.0)^{gs}, *O. couesi* (69.3)^{gs}, *O. devius* (60.5)^{gs}, *O. dimidiatus* (53.9)^{gs}, *O. gorgasi* (60.5)^{gs}, *O. hammondi* (60.5)^{gs}, *O. intectus* (60.5)^{gs}, *O. intermedius* (91.0)^{gs}, *O. keaysi* (58.3)^{gs}, *O. levipes* (60.5)^{gs}, *O. macconnelli* (58.0)^{gs}, *O. melanotis* (50.0)^{gs}, *O. nitidus* (55.2)^{gs}, *O. palustris* (53.9)^{gs}, *O. polius* (60.5)^{gs}, *O. rhabdops* (33.3)^{gs}, *O. rostratus* (50.0)^{gs}, *O. saturatior* (33.3)^{gs}, *O. subflavus* (50.0)^{gs}, *O. talamancae* (55.0)^{gs}, *O. xantheolus* (79.8)^{gs}, *O. yunganus* (60.5)^{gs}, *Osgoodomys banderanus* (50.0)^{gs}, *Otonyctomys hatti* (36.2)^{gs}, *Ototylomys phyllotis* (120.0)^{gs}, *Ovibos moschatus* (368502.1), *Ovis canadensis* (74644.9)^{eu}, *O. dalli* (55650.6)^{eu}, *Oxymycterus akodontius* (68.0)^{gs}, *O. angularis* (68.0)^{gs}, *O. delator* (81.5)^{gs}, *O. hiska* (68.0)^{gs}, *O. hispidus* (36.8)^{gs}, *O. hucucha* (68.0)^{gs}, *O. iheringi* (43.0)^{gs}, *O. inca* (35.0)^{gs}, *O. nasutus* (68.0)^{gs}, *O. paramensis* (42.0)^{gs}, *O. roberti* (83.4)^{gs}, *O. rufus* (75.4)^{gs}, *Ozotoceros bezoarticus* (40000.0)^{gs}, *Panthera onca* (100000.0)^{eu}, *Pappogeomys alcorni* (150.0), *P. bulleri* (150.0), *P. castanops* (251.8), *P. fumosus* (150.0), *P. merriami* (420.0), *Parascalops breweri* (51.0), *Pecari tajacu* (21266.7)^{gs}, *Perognathus alticola* (24.0), *P. amplus* (11.7), *P. fasciatus* (11.5), *P. flavescens* (8.8), *P. flavus* (7.7), *P. inornatus* (10.9), *P. longimembris* (7.6), *P. merriami* (6.8), *P. parvus* (21.8), *Peromyscus attwateri* (27.9)^{gs}, *P. aztecus* (40.0)^{gs}, *P. boylii* (21.4)^{gs}, *P. bullatus* (40.0)^{gs}, *P. californicus* (43.5)^{gs}, *P. crinitus* (18.0)^{gs}, *P. difficilis* (28.0)^{gs}, *P. eremicus* (23.6)^{gs}, *P. eva* (22.0)^{gs}, *P. furvus* (33.0)^{gs}, *P. gossypinus* (29.4)^{gs}, *P. grandis* (71.0)^{gs}, *P. gratus* (27.4)^{gs}, *P. guatemalensis* (40.0)^{gs}, *P. gymnotis* (40.0)^{gs}, *P. hooperi* (36.0)^{gs}, *P. leucopus* (21.2)^{gs}, *P. levipes* (21.4)^{gs}, *P. maniculatus* (21.3)^{gs}, *P. mayensis* (33.0)^{gs}, *P. megalops* (66.2)^{gs}, *P. mekisturus* (60.0)^{gs}, *P. melanocarpus* (59.0)^{gs}, *P. melanophrys* (40.0)^{gs}, *P. melanotis* (39.6)^{gs}, *P. melanurus* (40.0)^{gs}, *P. merriami* (40.0)^{gs}, *P. mexicanus* (32.6)^{gs}, *P. nasutus* (28.0)^{gs}, *P. ochraventer* (40.0)^{gs}, *P. pectoralis* (39.0)^{gs}, *P. perfulvus* (40.0)^{gs}, *P. polionotus* (13.0)^{gs}, *P. polius* (40.0)^{gs}, *P. pseudocrinitus* (18.0)^{gs}, *P. simulus* (40.0)^{gs}, *P. spicilegus* (36.0)^{gs}, *P. stirtoni* (29.2)^{gs}, *P. truei* (27.4)^{gs}, *P. winkelmanni* (40.0)^{gs}, *P. yucatanicus* (26.3)^{gs}, *P. zarhynchus* (40.0)^{gs}, *Phaenomys ferrugineus* (93.8)^{gs}, *Phenacomys intermedius* (25.2)^{gs}, *P. ungava* (32.5)^{gs}, *Philander andersoni* (325.0), *P. opossum* (750.0), *Phyllotis amicus* (20.2)^{gs}, *P. andium* (53.0)^{gs}, *P. bonaeriensis* (42.5)^{gs}, *P. caprinus* (50.8)^{gs}, *P. darwini* (50.8)^{gs}, *P. definitus* (89.0)^{gs}, *P. gerbillus* (17.4)^{gs}, *P. haggardi* (42.5)^{gs}, *P. magister* (68.5)^{gs}, *P. osgoodi* (45.1)^{gs}, *P. osilae* (49.0)^{gs}, *P. wolffsohni* (42.5)^{gs}, *P. xanthopygus* (56.3)^{gs}, *Pithecia aequatorialis* (2250.0)^{gn}, *P. albicans* (2800.0)^{gn}, *P. irrorata* (2241.0)^{gn}, *P. monachus* (1537.5)^{gn}, *P. pithecia* (1375.5)^{gn}, *Podomys floridanus* (30.8)^{gs}, *Potos flavus* (3000.0)^{gs}, *Priodontes maximus* (45359.7), *Procyon cancrivorus* (6949.9)^{gs}, *P. lotor* (5525.0)^{gs}, *Proechimys albispinus* (285.0), *P. brevicauda* (285.0), *P. canicollis* (285.0), *P. cayennensis* (316.0), *P. chrysaeolus* (285.0), *P. cuvieri* (330.0), *P. decumanus* (285.0), *P. dimidiatus* (167.6), *P. goeldii* (285.0), *P. guairae* (400.0), *P. hoplomyoides* (285.0), *P. iheringi* (203.5), *P. longicaudatus* (205.0), *P. magdalenae* (285.0), *P. mincae* (285.0), *P. myosuros* (285.0), *P. oconnelli* (285.0), *P. oris* (285.0), *P. poliopus* (285.0), *P. quadruplicatus* (285.0), *P. semispinosus* (360.5), *P. setosus* (285.0), *P. simonsi* (285.0), *P. steerei* (285.0), *P. urichi* (285.0), *Pseudalopex culpaeus* (9832.4)^{gs}, *P. griseus* (8280.0)^{gs}, *P. gymnocercus* (4690.0)^{gs}, *P. sechurae* (4000.0)^{gs}, *P. vetulus* (5350.0)^{gs}, *Pseudoryzomys simplex* (51.2)^{gs}, *Pteronura brasiliensis* (23999.9)^{gs}, *Pudu mephistophiles* (9600.0)^{gs}, *P. puda* (9749.9)^{gs}, *Puma concolor* (51600.0)^{gs}, *Punomys lemminus* (84.8)^{gs}, *Rangifer tarandus* (86034.0)^{eu}, *Reithrodon auritus* (70.9)^{gs}, *Reithrodontomys brevirostris* (12.9)^{gs}, *R. burti* (20.0)^{gs}, *R. chrysopsis* (19.0)^{gs}, *R. creper* (22.8)^{gs}, *R. darienensis* (13.0)^{gs}, *R. fulvescens* (11.4)^{gs}, *R. gracilis* (12.3)^{gs}, *R. hirsutus* (20.0)^{gs}, *R. humulis* (8.3)^{gs}, *R. megalotis* (9.4)^{gs}, *R. mexicanus* (19.0)^{gs}, *R. microdon* (20.0)^{gs}, *R. montanus* (10.9)^{gs}, *R. paradoxus* (12.9)^{gs}, *R. raviventris* (11.0)^{gs}, *R. rodriguezi* (20.0)^{gs}, *R. spectabilis* (19.0)^{gs}, *R. sumichrasti* (19.0)^{gs}, *R. tenuirostris* (20.0)^{gs}, *R. zacatecae* (9.4)^{gs}, *Rhagomys rufescens* (21.2)^{gs}, *Rheomys mexicanus* (40.0)^{gs}, *R. raptor* (38.0)^{gs}, *R. thomasi* (40.0)^{gs}, *R. underwoodi* (40.0)^{gs}, *Rhipidomys austrinus* (89.0)^{gs}, *R. caucensis* (89.0)^{gs}, *R. couesi* (89.0)^{gs}, *R. fulviventer* (89.0)^{gs}, *R. latimanus* (57.5)^{gs}, *R. leucodactylus* (80.0)^{gs}, *R. macconnelli* (41.6)^{gs}, *R. mastacalis* (77.5)^{gs}, *R. nitela* (89.0)^{gs}, *R. ochrogaster* (89.0)^{gs}, *R. venezuelae* (90.0)^{gs}, *R. venustus* (89.0)^{gs}, *R. wetzeli* (89.0)^{gs}, *Rhyncholestes raphanurus* (21.0), *Romerolagus diazi* (476.7), *Saguinus bicolor* (465.0)^{gn}, *S. fuscicollis* (387.0)^{gn}, *S. geoffroyi* (486.5)^{gn}, *S. imperator* (400.0)^{gn}, *S. inustus* (410.5)^{gn}, *S. labiatus* (575.0)^{gn}, *S. leucopus* (440.0)^{gn}, *S. midas* (540.0)^{gn}, *S. mystax* (618.0)^{gn}, *S. nigricollis* (462.0)^{gn}, *S. oedipus* (430.0)^{gn}, *S. tripartitus* (393.5)^{gn}, *Saimiri boliviensis* (615.0)^{gn}, *S. oerstedii* (278.5)^{gn}, *S. sciureus* (743.2)^{gn}, *S. ustus* (1000.0)^{gn}, *S. vanzolinii* (769.6)^{gn}, *Scalopus aquaticus* (91.3), *Scapanus latimanus* (55.0), *S. orarius* (61.2), *S. townsendii* (141.7), *Scapteromys tumidus* (146.0)^{gs}, *Sciurillus pusillus* (39.0)^{gs}, *Sciurus aestuans* (185.0)^{gs}, *S. alleni* (434.5)^{gs}, *S. arizonensis* (647.0)^{gs}, *S. aureogaster* (595.0)^{gs}, *S. carolinensis* (506.5)^{gs}, *S. colliaei* (498.0)^{gs}, *S. deppei* (190.0)^{gs}, *S. flammifer* (4293.0)^{gs}, *S. gilvigularis* (803.0)^{gs}, *S. granatensis* (250.0)^{gs}, *S. griseus* (731.0)^{gs}, *S. ignitus* (190.0)^{gs}, *S. igniventris* (700.0)^{gs}, *S. nayaritensis* (697.0)^{gs}, *S.*

niger (761.9)^{gs}, *S. oculatus* (650.0)^{gs}, *S. pucheranii* (803.0)^{gs}, *S. pyrrhinus* (482.0)^{gs}, *S. richmondi* (205.0)^{gs}, *S. sanborni* (136.0)^{gs}, *S. spadiceus* (403.3)^{gs}, *S. stramineus* (433.3)^{gs}, *S. variegatoides* (485.0)^{gs}, *S. yucatanensis* (225.0)^{gs}, *Scolomys melanops* (26.5)^{gs}, *S. ucayalensis* (26.5)^{gs}, *Scotinomys teguina* (11.2)^{gs}, *S. xerampelinus* (15.0)^{gs}, *Sigmodon alleni* (179.0)^{gs}, *S. alstoni* (55.7)^{gs}, *S. arizonae* (198.0)^{gs}, *S. fulviventer* (214.0)^{gs}, *S. hispidus* (92.4)^{gs}, *S. inopinatus* (140.5)^{gs}, *S. leucotis* (135.5)^{gs}, *S. mascotensis* (120.0)^{gs}, *S. ochrognathus* (122.0)^{gs}, *S. peruanus* (92.4)^{gs}, *Sigmodontomys alfari* (60.0)^{gs}, *S. aphrastus* (60.0)^{gs}, *Sorex arcticus* (8.2), *S. arizonae* (2.4), *S. bairdii* (8.3), *S. bendirii* (16.1), *S. cinereus* (4.7), *S. dispar* (5.0), *S. fumeus* (7.7), *S. haydeni* (4.0), *S. hoyi* (2.6), *S. longirostris* (3.6), *S. merriami* (5.9), *S. minutissimus* (3.0), *S. monticolus* (5.3), *S. nanus* (2.4), *S. ornatus* (5.0), *S. pacificus* (6.7), *S. palustris* (13.4), *S. preblei* (3.1), *S. tenellus* (3.7), *S. trowbridgii* (3.8), *S. tundrensis* (3.0), *S. ugyunak* (3.6), *S. vagrans* (4.4), *Spalacopus cyanus* (127.5), *Speothos venaticus* (6000.0)^{gs}, *Spermophilus adocetus* (125.0), *S. annulatus* (500.0), *S. armatus* (313.0), *S. atricapillus* (551.0), *S. beecheyi* (578.5), *S. beldingi* (280.5), *S. brunneus* (300.0), *S. canus* (213.0), *S. columbianus* (493.0), *S. elegans* (453.6), *S. franklinii* (363.0), *S. lateralis* (191.0), *S. madrensis* (275.0), *S. mexicanus* (189.6), *S. mohavensis* (190.0), *S. mollis* (165.4), *S. parryii* (760.0), *S. perotensis* (140.0), *S. richardsonii* (406.0), *S. saturatus* (220.0), *S. spilosoma* (89.0), *S. tereticaudus* (156.5), *S. townsendii* (213.0), *S. tridecemlineatus* (131.7), *S. variegatus* (691.6), *S. washingtoni* (207.5), *Sphiggurus insidiosus* (1000.0)^{gn}, *S. mexicanus* (2000.0)^{gn}, *S. spinosus* (750.8)^{gn}, *S. vestitus* (736.0)^{gn}, *S. villosus* (1750.0)^{gn}, *Spilogale putorius* (341.0), *S. pygmaea* (235.0), *Sylvilagus aquaticus* (2135.8)^{gs}, *S. audubonii* (889.6)^{gs}, *S. bachmani* (643.3)^{gs}, *S. brasiliensis* (950.0)^{gs}, *S. cunicularius* (3000.0)^{gs}, *S. dicei* (950.0)^{gs}, *S. floridanus* (1172.8)^{gs}, *S. insonus* (3000.0)^{gs}, *S. nuttallii* (755.1)^{gs}, *S. palustris* (1500.0)^{gs}, *S. transitionalis* (656.7)^{gs}, *Synaptomys borealis* (21.3)^{eu}, *S. cooperi* (31.9)^{eu}, *Syntheosciurus brochus* (138.8), *Tamandua mexicana* (4210.0)^{gn}, *T. tetradactyla* (5515.1)^{gn}, *Tamias alpinus* (36.6), *T. amoenus* (50.5), *T. bulleri* (100.0), *T. canipes* (70.4), *T. cinereicollis* (61.7), *T. dorsalis* (71.1), *T. durangae* (85.0), *T. merriami* (74.8), *T. minimus* (135.3), *T. obscurus* (73.0), *T. ochrogenys* (91.7), *T. palmeri* (69.4), *T. panamintinus* (52.3), *T. quadrimaculatus* (85.2), *T. quadrivittatus* (62.2), *T. ruficaudus* (68.0), *T. rufus* (53.6), *T. senex* (89.3), *T. siskiyou* (75.0), *T. sonomae* (75.0), *T. speciosus* (62.0), *T. striatus* (111.9), *T. townsendii* (74.8), *T. umbrinus* (63.0), *Tamiasciurus douglasii* (225.0), *T. hudsonicus* (201.2), *T. mearnsi* (225.0), *Tapirus bairdii* (299999.1)^{gs}, *T. pinchaque* (148949.8)^{gs}, *T. terrestris* (207500.9)^{gs}, *Taxidea taxus* (7107.6), *Tayassu pecari* (32233.7)^{gs}, *Thalpomys cerradensis* (24.0)^{gs}, *T. lasiotis* (24.0)^{gs}, *Thomasomys aureus* (88.0)^{gs}, *T. baeops* (77.0)^{gs}, *T. bombycinus* (114.5)^{gs}, *T. cinereiventer* (77.0)^{gs}, *T. cinereus* (77.0)^{gs}, *T. daphne* (77.0)^{gs}, *T. eleusis* (77.0)^{gs}, *T. gracilis* (77.0)^{gs}, *T. hylophilus* (77.0)^{gs}, *T. incanus* (77.0)^{gs}, *T. ischyurus* (77.0)^{gs}, *T. kalinowskii* (77.0)^{gs}, *T. ladewi* (77.0)^{gs}, *T. laniger* (35.5)^{gs}, *T. monochromos* (77.0)^{gs}, *T. niveipes* (77.0)^{gs}, *T. notatus* (77.0)^{gs}, *T. oreas* (77.3)^{gs}, *T. paramorum* (77.0)^{gs}, *T. pyrrhonotus* (77.0)^{gs}, *T. rhoadsi* (77.0)^{gs}, *T. rosalinda* (77.0)^{gs}, *T. silvestris* (77.0)^{gs}, *T. taczanowskii* (77.0)^{gs}, *T. vestitus* (76.5)^{gs}, *Thomomys bottae* (114.7), *T. bulbivorus* (359.9), *T. mazama* (75.0), *T. monticola* (80.0), *T. talpoides* (130.1), *T. townsendii* (263.4), *T. umbrinus* (166.0), *Thrichomys apereoides* (275.0), *Thylamys elegans* (28.9), *T. macrura* (20.7), *T. pallidior* (14.9), *T. pusilla* (41.0), *Tolypeutes matacus* (1200.0), *T. tricinctus* (1487.0), *Tremarctos ornatus* (140000.6)^{gs}, *Tylomys bullaris* (280.0)^{gs}, *T. fulviventer* (183.6)^{gs}, *T. mirae* (183.6)^{gs}, *T. nudicaudus* (100.0)^{gs}, *T. panamensis* (183.6)^{gs}, *T. tumbalensis* (280.0)^{gs}, *T. watsoni* (183.6)^{gs}, *Tympanoctomys barrerae* (70.0), *Urocyon cinereoargenteus* (3833.7)^{gs}, *Ursus americanus* (99949.4)^{eu}, *U. arctos* (139440.8)^{eu}, *Vicugna vicugna* (47499.6)^{gs}, *Vulpes velox* (2197.5), *V. vulpes* (4131.7), *Wiedomys pyrrhorhinos* (46.7)^{gs}, *Wilfredomys oenax* (46.8)^{gs}, *W. pictipes* (22.9)^{gs}, *Xenomys nelsoni* (130.0)^{gs}, *Zaedyus pichiy* (1380.0), *Zapus hudsonius* (17.1), *Z. princeps* (29.0), *Z. trinotatus* (27.5), *Zygodontomys brevicauda* (52.2)^{gs}, *Z. brunneus* (75.6)^{gs}, *Zygogeomys trichopus* (500.0),

Appendix 2

Moran's I correlograms showing phylogenetic autocorrelation in observed body size patterns for all species (a), allochthon species (b) and autochthon species (c). The distance intervals at which Moran's I values are calculated differs among groups since they are defined with equal number of pairs of species.

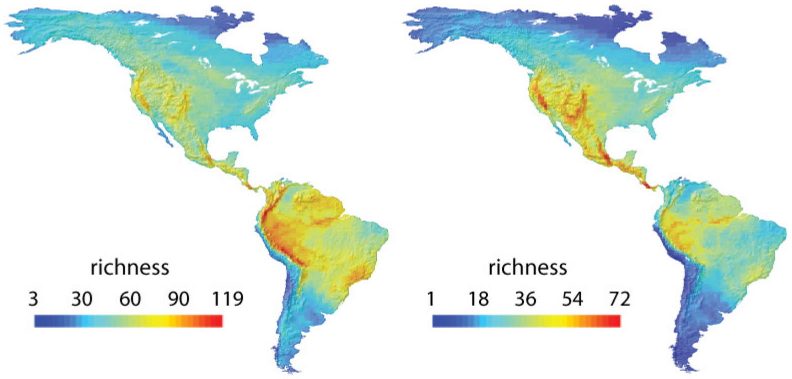


Appendix 3

Species richness geographical patterns of all species (a), autochthon species (b), allochthon species belonging to genera involved in the GABI (c), and species belonging to genera migrated from Eurasia through Beringia (d). An inset is used to reflect the species richness of the North American distribution of the GABI allochthons in South America (e).

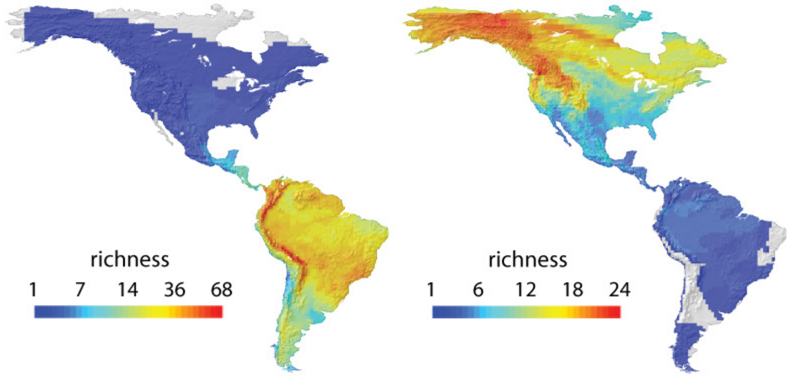
(a) all species

(b) autochthon species

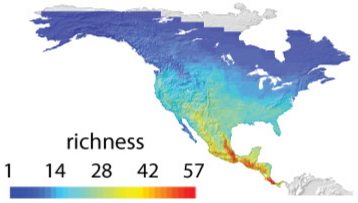


(c) GABI allochthon species

(d) eurasian allochthon species

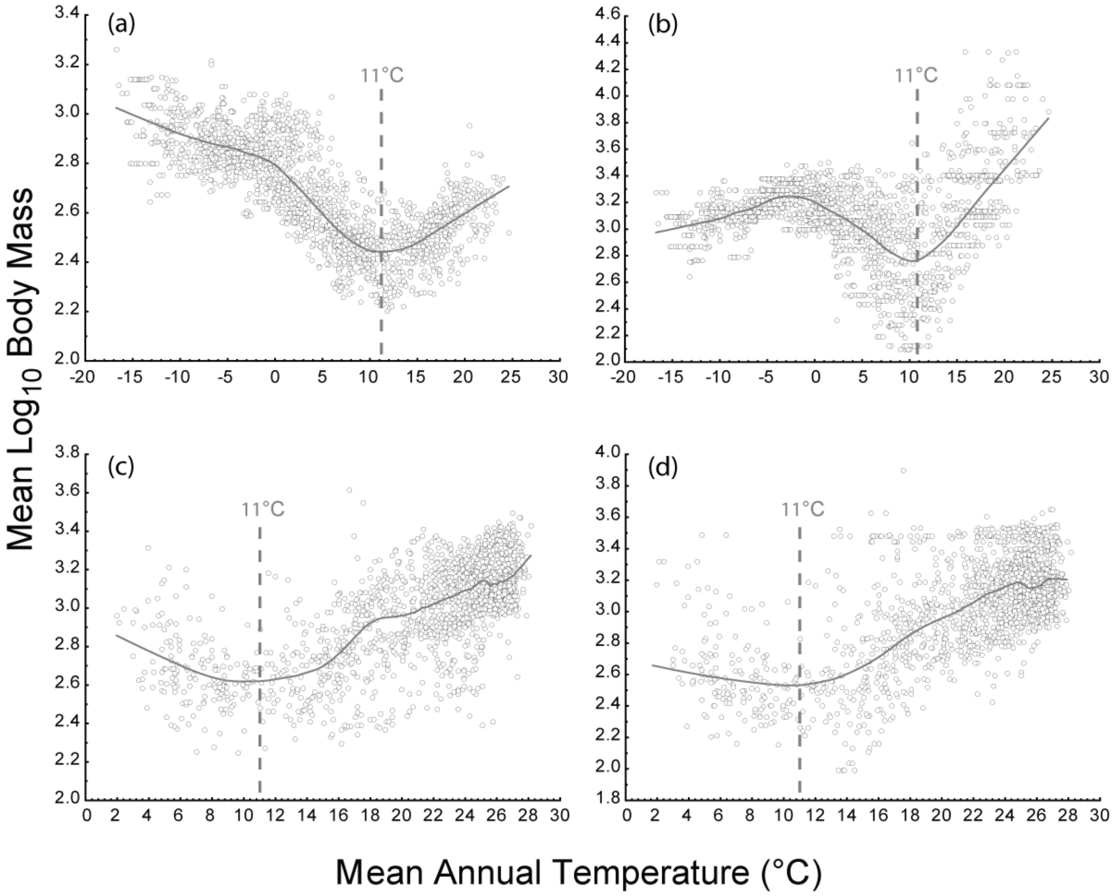


(e) GABI autochthons of North America



Appendix 4

Scatterplots of mean log-10 body mass against mean annual temperature for all species (a) and Eurasian allochthons (b) in the Nearctic, and for all species (c) and GABI allochthons (d) in the Neotropics. Lowess regression fits were used to identify at what temperature the relationships with temperature shift. Shifts in relationships are found near 11°C and are proximal to the temperature thresholds identified by Rodríguez *et al.* (2008).



Appendix 5

OLS three-variable environmental models for body mass of all species and allochthon species using mean annual temperature (TEMP), mean annual net primary productivity (NPP) and range in elevation (RIE). Models are performed below and above temperature values where relationships with temperature shift as confirmed by lowess regressions (i.e. ~11°C, see Appendix 4). Models for allochthon species are only conducted for Eurasian allochthons in the Nearctic and GABI allochthons in the Neotropics. Bold regression coefficients indicate the primary predictor in each model.

Region	Group	TEMP	NPP	RIE	R^2
Nearctic	All species				
	below 11°C	**-0.800**	0.015	0.123	0.610
	above 11°C	**0.578**	-0.190	-0.380	0.442
	Eurasian-allochthons				
	below 11°C	**-0.340**	-0.130	0.276	0.253
	above 11°C	**0.606**	-0.280	0.277	0.663
Neotropics	All species				
	below 11°C	**-0.360**	-0.130	0.069	0.157
	above 11°C	**0.545**	-0.070	-0.320	0.489
	GABI-allochthons				
	below 11°C	-0.330	-0.150	**0.345**	0.293
	above 11°C	**0.757**	-0.230	-0.010	0.397

Appendix 6

Three-variable environmental OLS regressions for mean log10-body size including all its spatial autocorrelation in the set of predictors. The spatial structure of body size that is not accounted by mean annual temperature (TEMP), mean annual net primary productivity (NPP) and range in elevation (RIE), is included as an additional independent variable (Independent spatial variation) in the models. Residual spatial autocorrelation was eliminated in all cases (Moran's $I \leq 0.05$) and thus standardized regression coefficients can be compared with those from OLS models not including any spatial variable (Table 1). Partial regression indicating the amounts of variation in body size explained by the environmental variables (R^2env), the variation explained by other sources of spatial variation (R^2spa) and the variation which is not spatially structured (R^2non-spa) are also shown. The spatial variation variable shows the highest standardized coefficients except for all species in the Nearctic and allochthon species in the Neotropics, indicating that the set of sources of spatial variation in body size not accounted by our predictors are of importance to explain body size spatial variation. Acknowledging that, both the rank and sign of the predictors from OLS models (Table 1) remain robust once spatial filters are included and residual spatial autocorrelation is removed.

Region	Group	n	TEMP	NPP	RIE	Independent spatial variation	R²env+spa	R²env	R²spa	R²non-spa
Nearctic	All species	508	-0.646	-0.139	0.001	0.592	0.897	0.546	0.351	0.103
	Autochthons	429	-0.325	-0.134	-0.113	0.753	0.754	0.186	0.568	0.246
	Eurasian-allochthons	56	0.335	-0.477	0.183	0.785	0.827	0.211	0.616	0.173
	GABI-allochthons	19	-0.462	-0.412	0.062	0.534	0.904	0.619	0.285	0.096
Neotropics	All	669	0.508	-0.012	-0.300	0.628	0.898	0.503	0.394	0.102
	Autochthons	322	0.040	0.104	-0.398	0.766	0.820	0.233	0.587	0.180
	GABI-allochthons	347	0.793	-0.187	0.014	0.689	0.898	0.426	0.472	0.102

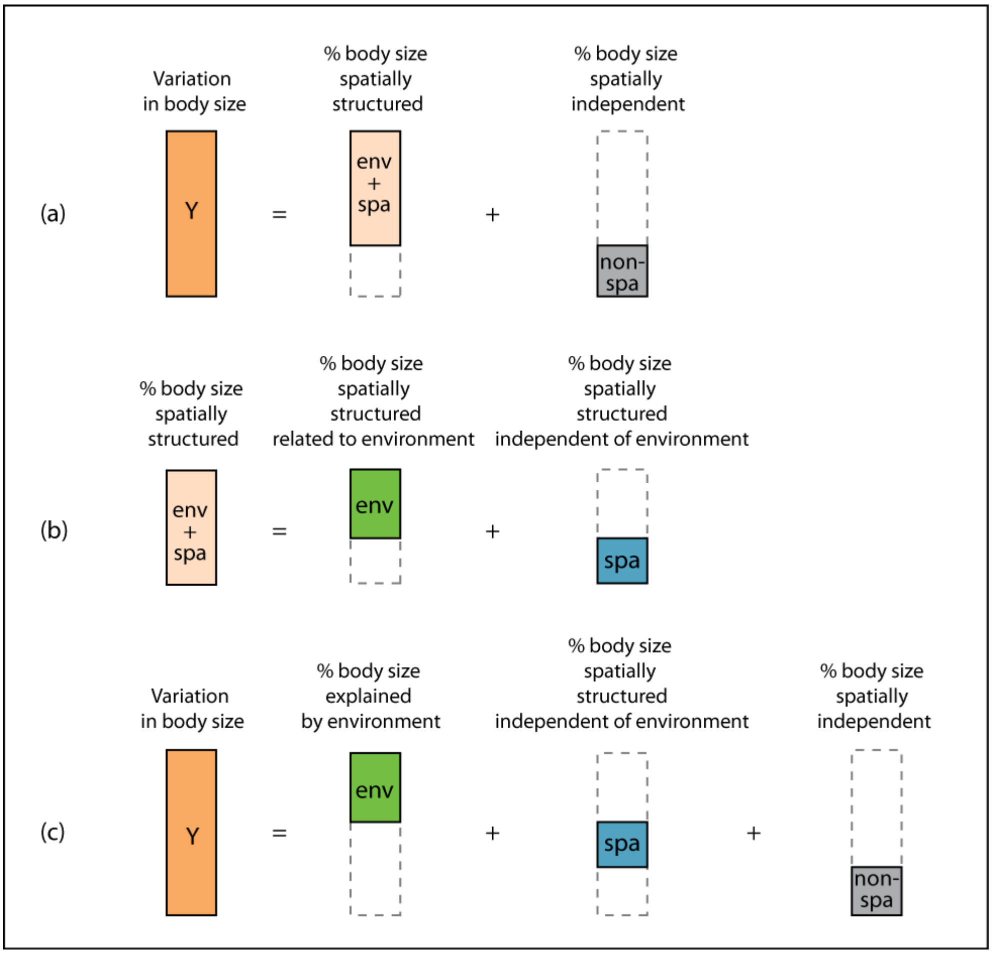


Figure S6. Spatial filtering procedure to include spatial structure independent from the trait. First, spatial filters are selected for body size using the Griffith and Peres-Neto (2006) algorithm, and used as predictors in a regression that yields the proportion of body size that is spatially autocorrelated (a). Second, that proportion of spatially autocorrelated body size is regressed against the environmental predictors to obtain the residuals, that is, the proportion of spatially structured body size independent from the environment (b). Those residuals are finally included as a predictor in the models (c).

6. Conclusiones generales

Conclusiones generales

- Entender los mecanismos que intervienen en la configuración de los patrones de diversidad que observamos en la actualidad requiere apreciar procesos evolutivos (especiación/extinción), así como cambios históricos en la paleogeografía o el paleoclima, responsables de ciertos eventos de dispersión ocurridos en el pasado. Para incorporar aspectos evolutivos e históricos en los estudios macroecológicos pueden utilizarse diversas líneas de evidencia (p.e. paleoclima, paleogeografía, registro fósil, análisis filogenéticos, información de intercambios bióticos), que a pesar de presentar limitaciones nos permiten aproximar dichos aspectos.

- La conservación de nicho constituye un marco teórico válido para interpretar las relaciones de distintos patrones biogeográficos con el ambiente, con procesos evolutivos y con eventos históricos. Aunque no es posible realizar experimentos a escalas biogeográficas, en base a los mecanismos que propone la conservación de nicho pueden realizarse predicciones susceptibles de ser testadas.

- La incorporación en el estudio de patrones biogeográficos de rasgos biológicos asociados a la historia de vida de las biotas, como por ejemplo la capacidad dispersora, ayudará a alcanzar un mejor entendimiento de los procesos que generan dichos patrones.

Capítulo 2. Conservación de nicho y riqueza de especies de reptiles

- Para entender los patrones de riqueza de especies de reptiles en África, es preciso tener en cuenta los momentos en que se originaron los distintos clados, las condiciones paleoclimáticas en dichos momentos, así como información referida a la distribución de los ancestros de las especies actuales obtenida a partir del registro fósil.

- La conservación de nicho es capaz de explicar las asociaciones que se observan actualmente entre los gradientes de riqueza de especies y el clima. Esta observación, común para diversos grupos taxonómicos en ambientes tropicales húmedos (conservación de nicho tropical), se revela como cierta también para grupos de reptiles que muestran mayor riqueza de especies en ambientes áridos y cuyos ancestros se originaron ante esas condiciones.

- El papel de los desiertos en el estudio de patrones biogeográficos podría ser relevante para testar la conservación de nicho, si se demostrase que otros grupos de organismos originados en ambientes desérticos presenten mayores niveles de riqueza de especies en estos ambientes.

- La exploración del registro fósil en relación a reconstrucciones paleoclimáticas puede ser útil para establecer la existencia de la conservación de nicho en ausencia de datos filogenéticos con alta resolución.

Capítulo 3. Componentes evolutivas del tamaño de rango en aves oscines

- El tamaño del rango geográfico de aves oscines presenta una señal filogenética baja a moderada pero claramente estructurada en el espacio, indicando que las relaciones evolutivas intervienen en la configuración del tamaño de rango geográfico tanto a nivel de especie como a nivel de ensamblaje.

- El patrón de regla de Rapoport que se observa en Norteamérica no es un artefacto derivado de la presencia de especies migratorias (debido a sus amplios rangos de distribución) ya que el patrón también se encuentra para los rangos estivales de las especies migratorias y para las especies que no migran. Éstas son pocas en número, están cercanamente emparentadas y muestran grandes rangos predichos con base a las relaciones filogenéticas.

- Aunque los factores ambientales son capaces de explicar entre un 40 y un 65% de la variación en las componentes filogenética y no filogenética del tamaño de rango, los patrones son distintos en Norteamérica y Suramérica independientemente de qué tipo de rango geográfico se estudie (reproductivo o no reproductivo). Esto está relacionado con las diferencias climáticas y geográficas que existen en ambos continentes.

- En Sudamérica la señal filogenética es equivalente a la señal no filogenética para los rangos no reproductivos, mostrando que el conjunto de especies de aves oscines que migran hacia el Sur muestran fuertes estructuras filogenéticas que podrían estar asociadas a otros rasgos biológicos como la capacidad dispersora. La inclusión de éste y otros rasgos biológicos en estudios futuros posibilitará un entendimiento más completo de las causas que subyacen a la biogeografía del tamaño de rango.

Capítulo 4. Gradiente global de tamaño corporal de aves

- La regla de Bergmann (1847) no es suficiente para explicar los patrones de tamaño corporal de aves. La elevada señal filogenética encontrada en niveles basales de la filogenia, indican un papel fundamental de la historia evolutiva de las biotas a la hora de configurar los gradientes de tamaño corporal.

- La señal filogenética para el tamaño corporal de aves se manifiesta en niveles profundos de la filogenia (nivel de familia), lo que apunta hacia la necesidad de incluir análisis filogenéticos de forma explícita a la hora de estudiar este rasgo.

- Las hipótesis de tamaño corporal no son excluyentes, sino que se complementan en distintas partes del mundo. La hipótesis de resistencia a la escasez de recursos explica parte del gradiente global de tamaño corporal de aves, bien en combinación con la hipótesis de conservación de calor en el Nuevo Mundo, o en combinación con los efectos de la estacionalidad en el Viejo Mundo. Las interacciones bióticas representadas por la riqueza de especies no muestran efectos sobre el tamaño corporal de forma independiente a la variación ambiental.

- La complejidad geográfica de los patrones indica que para entender las diferencias regionales será necesaria información más detallada de los patrones espaciales de diversificación y de la historia biogeográfica de los principales grupos de aves.

Capítulo 5. Migraciones cenozoicas y tamaño corporal de mamíferos

- Eventos históricos de dispersión tales como los intercambios bióticos ocurridos en el Plio-Pleistoceno, contribuyen a explicar el gradiente de tamaño corporal de los mamíferos del Nuevo Mundo de forma diferenciada en distintas regiones. Esto es, parte del patrón de Bergmann observado en las regiones más septentrionales se debe a la influencia de especies pertenecientes a géneros de gran tamaño que llegaron cruzando el estrecho de Bering y parte de los tamaños reducidos que se encuentran en regiones meridionales y a lo largo de los Andes se deben a especies que llegaron a Sudamérica gracias al Gran Intercambio Biótico Americano.

- El tiempo que los distintos géneros han permanecido en las distintas regiones de las Américas permite interpretar las diferencias en cuanto a la señal filogenética y la intensidad de las relaciones con el ambiente que se observan entre especies derivadas de géneros autóctonos y alóctonos.

- La capacidad de dispersión de los distintos clados está relacionada con el tamaño corporal y por tanto podría ser el rasgo biológico conservado filogenéticamente. Esto apunta hacia la necesidad de tener en cuenta la capacidad dispersora en próximas investigaciones.