

Growing empirical evidence suggests we lack a coherent understanding of the decision rules governing mate choice. Rational choice models have proven fruitful for static or otherwise simple selection scenarios, and yet may prove inadequate for generating accurate predictions of how sexually selected male traits evolve by female mate choice in the socially dynamic sexual marketplace. Further elucidating complex but predictable mate choice patterns would generate valuable insight into the evolution of decision-making and the coevolutionary processes of sexual selection.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Fig. S1

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LIFE HISTORY

Age-related mortality explains life history strategies of tropical and temperate songbirds

Thomas E. Martin

Life history theory attempts to explain why species differ in offspring number and quality, growth rate, and parental effort. I show that unappreciated interactions of these traits in response to age-related mortality risk challenge traditional perspectives and explain life history evolution in songbirds. Counter to a long-standing paradigm, tropical songbirds grow at similar overall rates to temperate species but grow wings relatively faster. These growth tactics are favored by predation risk, both in and after leaving the nest, and are facilitated by greater provisioning of individual offspring by parents. Increased provisioning of individual offspring depends on partitioning effort among fewer young because of constraints on effort from adult and nest mortality. These growth and provisioning responses to mortality risk finally explain the conundrum of small clutch sizes of tropical birds.

Life history strategies of virtually all taxa vary along a slow-fast gradient. Slow strategies are characterized by slow growth, low total parental effort for fewer offspring but high effort per offspring [i.e., high parental investment (1)], and long life (2). Fast strategies are characterized by the opposite (2). This slow-fast gradient is particularly well defined for songbirds of different latitudes, with tropical songbirds typically on the slow end and northern temperate birds falling toward the fast end (3–7). An extensive body of work and theory has attempted to explain the drivers of this pattern of life history variation, yet no consensus has emerged (8–13).

An early perspective on latitudinal variation in life history strategies proposed that stable tropical environments allow habitats to become “saturated” with individuals, thereby favoring slow life history strategies that improve competitive abilities (10, 11). Yet the life history traits of coexisting tropical songbird species can vary as much or even more (5, 14) than those of temperate species, and this variation is difficult to explain by the simple argument that competition is greater in the tropics. Other hypotheses invoking latitudinal differences in food limitation or nest predation have also failed to explain latitudinal variation (4–6). Differences in parental effort within and among latitudes have been addressed in part by classic theories based on age-specific or season-specific mortality [e.g., (8, 9, 12, 13)]. However, an explanation is lacking for why effort may be partitioned among differing numbers of young and how this integrates with enigmatic growth strategies among species and latitudes. In short, the causes of variation in growth strategies, parental provisioning rates, and clutch size within and among latitudes remain unclear.

Here, I provide a conceptual framework for within- and across-latitude variation in life history strategies based on mortality risk across life stages (Fig. 1). I base this on empirical evidence from extensive field studies of 20 to 30 coexisting songbird species in each of three locations: north temperate Arizona, USA, and tropical Malaysia and Venezuela.

An initial enigma is presented by the slow growth of tropical songbirds. Predation causes the vast majority of mortality for songbird offspring in the nest (nestlings) (15). Higher risk of nest predation favors faster growth (Fig. 2A and table S1A) in order to reduce time in the nest (nestling period) and exposure to nest predators (Fig. 1) (5, 16). Yet tropical birds exhibit slower growth rates than temperate species for similar or even higher nest predation rates (Fig. 2A and table S1A), which has been perceived as a paradox (9). Moreover, this paradox was reinforced by the inability of an assumed longevity benefit to explain the slower growth of tropical birds (17).

This apparent paradox may reflect the way that growth rates have been viewed and estimated. Traditional growth rate estimates (5, 7, 17) provide estimates of peak growth (18). Slower peak growth rates of tropical birds have been implicitly assumed to reflect slower overall growth. Yet nestling periods of tropical species are 2 to 6 days shorter for the same peak growth rates (K_1) as temperate species (Fig. 2B and table S1B). If slower peak growth reflects slower overall growth, it should cause tropical offspring to leave the nest (fledge) at smaller relative sizes and earlier developmental states relative to temperate species (Fig. 3A, dashed versus yellow curves). Yet reduced development at fledging increases subsequent mortality (19). Tropical species might minimize such costs by extending the nestling period, but that increases nest predation risk (16) and is not reflected by the relationship of nestling period with peak growth rates (Fig. 2B). I suggest that this conundrum can be resolved by considering a

U.S. Geological Survey, Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT 59812, USA.

E-mail: tom.martin@umontana.edu

heretofore unrecognized possibility that tropical birds use an alternative growth trajectory. Specifically, tropical birds exhibit slower peak growth rates but faster growth at later ages, thereby achieving a relative size similar to that of tem-

perate species without extending the nestling period (solid black versus yellow curves in Fig. 3A).

A pair of wren (Troglodytidae) species illustrates common differences in tropical-temperate

growth trajectories. Growth is faster in the temperate species at early ages (the yellow curve in Fig. 3B rises faster). However, the faster growth of the tropical wren at later ages allows it to achieve the same relative body mass as the temperate wren in the same amount of time (Fig. 3B). These differences are illustrated more clearly by calculating instantaneous growth rates over the nestling period (Fig. 3C). A series of tropical and temperate species paired by phylogeny shows that growth rates are higher for temperate species than for their tropical relatives in the early nestling period through peak growth (yellow above black curves in Fig. 3, C to I). The lower peak rates of tropical species (Fig. 3, C to I) reflect the paradigm of slow growth in the tropics (5, 7, 17). However, growth rates of tropical species also consistently exceed temperate species after their peak (black above yellow curves in Fig. 3, C to I). The growth trajectory of tropical birds allows them to often achieve a similar average growth rate over the entire nestling period (K_{avg} ; Fig. 3, C to G) and similar relative size at fledging as temperate relatives without extending the length of the nestling period (e.g., Fig. 3B). Indeed, relative body mass at fledging does not differ between tropical and temperate birds for the same nestling period (Fig. 4A and table S2A). The ability to achieve similar fledging mass without increasing the length of the nestling period is critical because it means that tropical birds do not increase their risk of nest predation through longer nestling periods. Of course, in some cases, tropical species grow slower overall and extend the nestling period (Fig. 3, H and I), but these generally are species with lower nest predation risk (Fig. 2A).

The lower peak but more sustained growth of many tropical birds (Fig. 3) may be important for aiding wing growth and flight capabilities after fledging (Fig. 1). Enhanced locomotor performance aids escape from predators across taxa (20, 21) and can result from slower and steadier mass growth (22), as is typical of tropical birds (Fig. 3). Partially developed wings can help offspring to escape predators (23)—commonly the primary source of fledgling mortality in songbirds (19)—and longer, more developed wings increase fledglings' ability to evade predators (19, 24). Longer wings can be achieved through longer nestling periods (19, 24), but that increases nest predation risk (16) and creates a trade-off in predation risk between nestling and fledgling stages (Fig. 1). This trade-off can be resolved by a growth strategy (i.e., lower peak, more sustained growth) that allows enhanced wing growth without lengthening the time in the nest and exposed to nest predators. Indeed, tropical birds exhibit faster wing growth (Fig. 4B and table S2B), allowing them to fledge with longer wings than temperate birds for the same nestling period (Fig. 4C and table S2C). Thus, relative to temperate birds, tropical species enhance growth of a locomotor trait that can reduce mortality risk after leaving the nest (19, 24) without increasing mortality risk in the nest.

Given the survival advantage that more developed wings provide fledglings (19, 24), we might

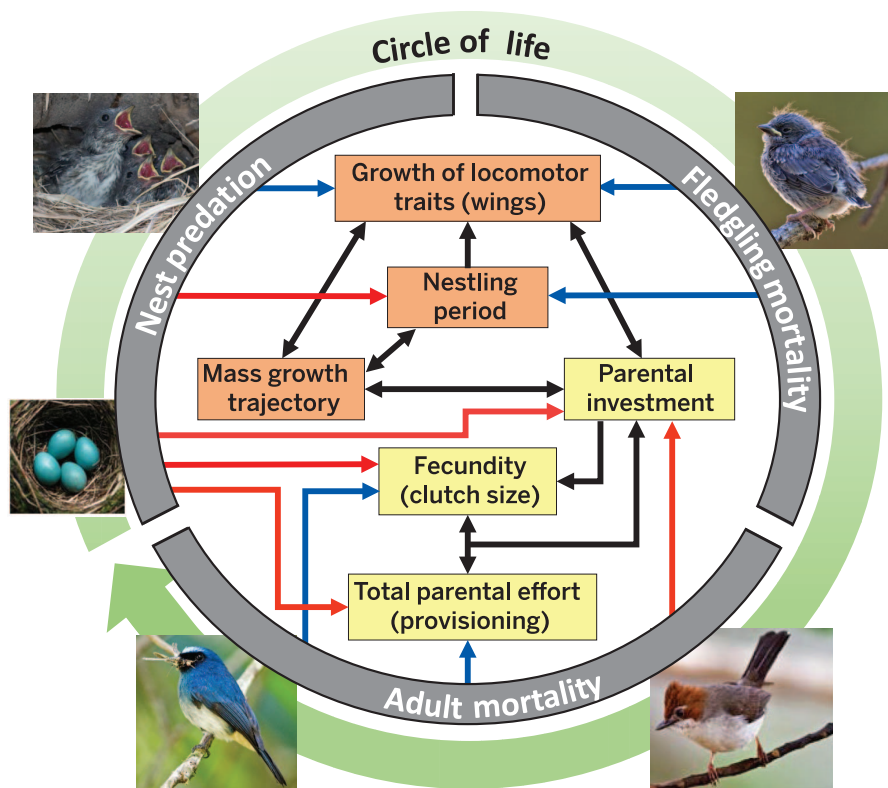


Fig. 1. Conceptual framework for life history strategies. Over the circle of life, mortality risk varies across life stages (gray ring) and exerts selection on growth strategies (orange boxes) and parental strategies (yellow boxes). Blue arrows reflect positive selection; red arrows reflect negative selection; black arrows reflect the influence of life history traits on each other. Nest and fledgling predation exert opposing selection on length of the nestling period. Fledgling predation risk favors longer nestling development to enhance locomotor traits (i.e., longer wings), but longer periods increase nest predation risk. Increased parental investment and steady mass growth allow enhanced wing growth without extending the length of the nestling period and increasing predation risk. Parental investment is a function of total parental effort (total provisioning rate) partitioned among young, where total parental effort is a result of adult and nest mortality. The higher parental investment that facilitates the longer wings favored in tropical birds is achieved by small clutch sizes.

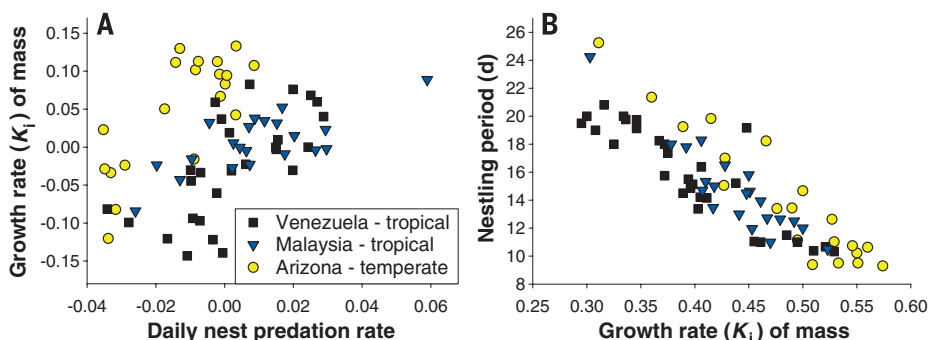


Fig. 2. Growth and nest predation on three continents. (A) Peak growth rate in species with higher nest predation risk but is slower in tropical species with the same level of risk as temperate species, while controlling for mass (table S1A). Growth rate is the conventional peak rate of growth, K_1 (see Fig. 3A). (B) Nestling period covaries with growth rate, but tropical species have shorter nestling periods for the same growth rate as temperate species (table S1B).

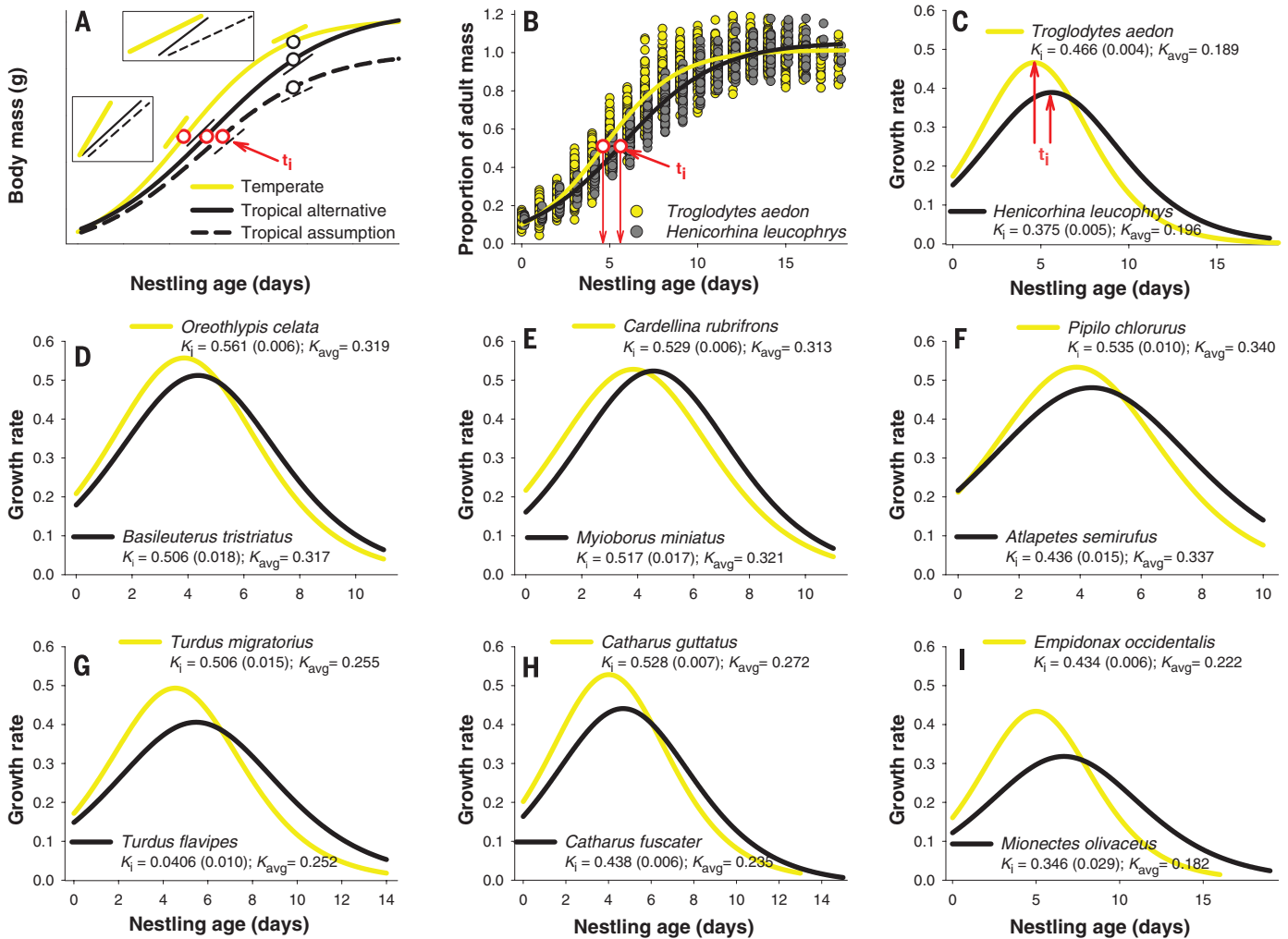


Fig. 3. Differences in growth trajectories of body mass of tropical versus temperate songbirds. (A) Conceptual characterization of possible growth trajectories [see also (18)]. Growth rate is estimated as the instantaneous slope (K_i depicted by the small lines) on the growth curve. The small lines representing slopes of differing growth trajectories are exaggerated in the boxes at two ages to illustrate the differences. Traditionally, estimates are made at the time (t_i) of the inflection point (red circles) where growth switches from accelerating to decelerating, which represents peak growth rate. However, growth rate may also differ at the late nestling stage (black circles). Tropical birds are assumed to have slower growth throughout the nestling period (dashed black curve), where slopes are shallower than for temperate birds (yellow curve) at both ages.

expect temperate birds to produce wings of comparable size. However, increased rates of energetically expensive wing growth may depend not only on a slower, more sustained growth strategy, but also on increased energy availability (Fig. 1) (25). The field data show that higher provisioning (food delivery) rates per offspring explain longer relative wing sizes within and across latitudes (Fig. 4D and table S2D). Thus, greater parental investment, commonly observed in tropical birds (4–6), can have critical fitness benefits through effects on offspring quality manifested by wing development and its consequences for survival of young after leaving the nest.

The reason that tropical and temperate species do not provision individual offspring at similar

rates arises in part from constraints of age-related mortality on provisioning effort (Fig. 1). Life history theory predicts that adult and offspring mortality should constrain parental effort (4, 5, 9, 12, 13). Indeed, variation in parental effort, reflected by total provisioning rate of all offspring, is explained by nest predation risk and adult mortality across species and latitudes (Fig. 4, E and F, and table S3A). Adult mortality is commonly lower for tropical birds (3, 17) and therefore is associated with lower overall provisioning rates (Fig. 4F).

The only way that tropical birds can increase provisioning rates per offspring, given mortality constraints on total provisioning, is through reduced clutch size. The smaller clutch size of trop-

ically birds indeed allows increased provisioning per offspring (Fig. 4G and table S3B), which enables growth of longer wings (Fig. 4D) to enhance fledging survival (19, 24) without extending the nestling period and increasing nest predation risk. The small clutch sizes of tropical birds have puzzled scientists for more than half a century, and these results finally explain it as an integrated function of growth and parental provisioning strategies in response to age-related mortality risk.

Temperate birds may not increase parental investment to enhance wing growth as much as tropical birds because of greater adult and juvenile (independent young after the fledging stage) mortality. Mortality rates of juvenile songbirds to the

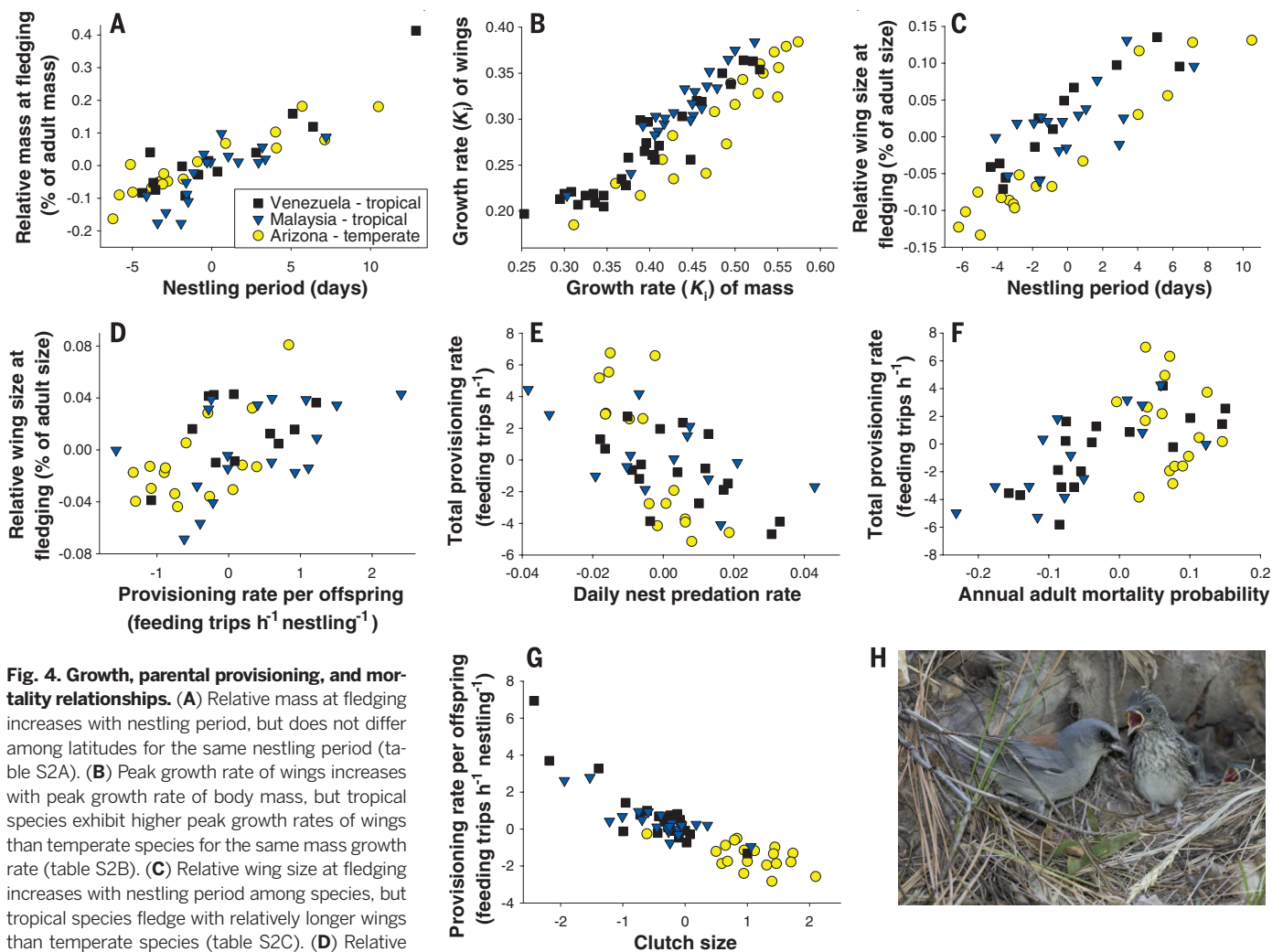


Fig. 4. Growth, parental provisioning, and mortality relationships. (A) Relative mass at fledging increases with nestling period, but does not differ among latitudes for the same nestling period (table S2A). (B) Peak growth rate of wings increases with peak growth rate of body mass, but tropical species exhibit higher peak growth rates of wings than temperate species for the same mass growth rate (table S2B). (C) Relative wing size at fledging increases with nestling period among species, but tropical species fledge with relatively longer wings than temperate species (table S2C). (D) Relative wing size at fledging increases with provisioning rate per offspring while controlling for other factors (table S2D). (E and F) Total provisioning rate decreases with nest predation risk (E) and increases with annual adult mortality probability (F) across species controlled for each other and other factors (table S3A). (G) Provisioning rate per offspring decreases with increasing clutch size, controlled for mass and total provisioning rate (table S3B). (H) A *Junco hyemalis* young taking its first steps to leave the nest and begging for food from its parent.

next breeding season, as well as adult mortality rates, are commonly higher in temperate than in tropical songbird species (3, 17, 26, 27). When adult and juvenile mortality are high, selection can favor a strategy of more, but lower-quality, young (2, 11–13). This hypothesis fits the patterns here because an increase in the number of offspring in the temperate zone comes at the expense of parental investment (Fig. 4G), and reduced parental investment produces lower-quality young, as reflected by shorter wing length (Fig. 4D). In short, temperate songbirds produce more young of lower quality, which is adaptive given their higher juvenile and adult mortality rates.

Mortality risk during different life stages can explain variation in the life history strategies of songbirds across latitudes (Fig. 1). Adult and offspring mortality have been theorized to influence parental effort across taxa (2, 9, 12, 13), and total provisioning rate (which reflects parental effort) is well explained by adult mortality and

nest predation risk in songbirds (Fig. 4, E and F). Consideration of mortality risk after leaving the nest (fledgling mortality) adds to our understanding of latitudinal variation in songbird life histories. In particular, seemingly paradoxical slower peak growth of tropical birds in the face of nest predation risk makes sense once their more sustained growth is recognized. The lower peak and sustained growth resolves the putative predation cost in the nest while allowing enhanced wing growth and survival after leaving the nest. Increased parental provisioning per offspring, achieved through reduced clutch size (Fig. 4G), further enhances wing growth (Fig. 4D) to benefit fledgling survival. Ultimately, selection by nest predation on growth rate and nestling period places constraints on the developmental stage at fledging (Fig. 2) (19) and creates a trade-off with subsequent fledgling survival. However, shifts in growth, fecundity, and parental provisioning strategies help to resolve this trade-off (Fig. 1). This interaction in mortality risk among

life stages, considered together with the interactions among life history traits (Fig. 1), is a basis for greater understanding of latitudinal variation in life history strategies.

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SUPPLEMENTARY MATERIALS

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 Materials and Methods
 Supplementary Text
 Fig. S1
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FUNGAL SYMBIONTS

Global assessment of arbuscular mycorrhizal fungus diversity reveals very low endemism

J. Davison,^{1*} M. Moora,^{1*} M. Öpik,^{1*} A. Adholey,² L. Ainsaar,¹ A. Bâ,³ S. Burla,² A. G. Diedhiou,⁴ I. Hiiesalu,^{1,5} T. Jairus,¹ N. C. Johnson,⁶ A. Kane,⁴ K. Koorem,^{1,7} M. Kochar,⁸ C. Ndiaye,⁴ M. Pärtel,¹ Ü. Reier,¹ Ü. Saks,¹ R. Singh,⁸ M. Vasar,¹ M. Zobel^{1*}

The global biogeography of microorganisms remains largely unknown, in contrast to the well-studied diversity patterns of macroorganisms. We used arbuscular mycorrhizal (AM) fungus DNA from 1014 plant-root samples collected worldwide to determine the global distribution of these plant symbionts. We found that AM fungal communities reflected local environmental conditions and the spatial distance between sites. However, despite AM fungi apparently possessing limited dispersal ability, we found 93% of taxa on multiple continents and 34% on all six continents surveyed. This contrasts with the high spatial turnover of other fungal taxa and with the endemism displayed by plants at the global scale. We suggest that the biogeography of AM fungi is driven by unexpectedly efficient dispersal, probably via both abiotic and biotic vectors, including humans.

The arbuscular mycorrhizal (AM) fungi (phylum Glomeromycota) are an ancient but species-poor group of root symbionts whose origin coincided with the first appearance of land plants (1). The AM symbiosis involves ~80% of land plants and ~250 morphologically defined or 350 to 1000 molecularly defined AM

fungi (2, 3). The relationship typically allows the fungus to receive plant-synthesized carbon, while conferring the plant with an increased capacity for nutrient capture and improved tolerance of drought and pathogens (4). At a wider scale, the symbiosis influences plant-plant interactions and the structure of plant communities, and thus it can affect agricultural production and the conservation and restoration of ecosystems (5). Because many AM fungi are unculturable, identification of AM fungal taxa in the environment is principally dependent on DNA-based methods; these asexual organisms are classified into approximately species-level taxonomic units using clustering or sequence-matching algorithms (6). The recent rapid development of DNA sequencing technology is allowing detection of increasing numbers of AM fungi and other microorganisms in environmental samples and enabling their responses to local and regional environmental gradients to be recorded (7–9). However, knowledge about global AM fungal diversity is piecemeal. This is partly because most classification approaches generate operational taxonomic units (OTUs) that cannot be readily compared between different studies or study areas (2, 10). Additionally, the communities of AM fungi present in many geographic regions, biomes, and ecosystems remain entirely unstudied (11, 12).

Although empirical data concerning AM fungal dispersal are limited, the process is believed to be mostly local and mediated by invertebrates (4, 13), with some evidence of small mammals, water, and human activities (e.g., agricultural practices) dispersing propagules farther (14–16). As yet, there is no direct evidence of efficient long-distance dispersal (13, 17). Hence, extensive global sampling of AM fungal diversity should reveal high endemism and similar responses to environmental conditions as those shown to drive local-scale diversity (7, 8). We used high-throughput sequencing of environmental samples to survey AM fungal diversity and distribution in natural ecosystems worldwide. We examined the contributions of environmental conditions, spatial distance between plots, paleogeographic history, and plant-host identity on AM fungal diversity at local to global scales.

We collected 1014 individual root samples from vegetation plots worldwide and identified DNA-based AM fungal taxa ["virtual taxa" (VT), after (10)] in plant roots by using 454 sequencing. VT are phylogenetically defined sequence groups that exhibit a taxonomic resolution similar to that of morphological species, or above that resolution in some AM fungal families (11). As in traditional binomial nomenclature, the VT classification applies consistent principles to taxonomic assignments across data sets and provides comparability between studies. We used 912,515 quality-filtered AM fungal reads, representing 836 samples, 161 plant species, and 67 plots, for further analysis (Fig. 1A, fig. S1, tables S1 to S3, and database S1). We recorded 236 (68%) of the 348 currently known AM fungal VT and identified a further 10 taxa that were previously undescribed (fig. S2). Ninety-three percent of recorded VT were present on more than one continent, and one-third (34%) were present on all six sampled continents. Furthermore, 90% of VT were found in more than one climatic zone, and 79% were found in both forests and grasslands (the two most widely sampled ecosystems) (Fig. 1B). We added published data on AM fungal VT distribution from the MaarjAM database (10) to create a comprehensive data set containing all available VT records. We compared this data set with the distribution of plants (the AM fungus host organisms) for which global data are available at the family (18) but not the species level. The mean fractions of the AM fungal taxon pool found on individual continents (57%) and of shared

¹Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, Tartu 51005, Estonia. ²Centre for Mycorrhizal Research, The Energy and Resources Institute (TERI), India Habitat Centre, Lodhi Road, New Delhi 110 003, India. ³Laboratoire des Symbioses Tropicales et Méditerranéennes, Unité Mixte de Recherche 113, Laboratoire de Biologie et Physiologie Végétales, Faculté des Sciences Exactes et Naturelles, Université des Antilles, BP 592, 97159, Pointe-à-Pitre, Guadeloupe (French West Indies). ⁴Laboratoire Commun de Microbiologie de l'Institut de Recherche pour le Développement–Institut Sénégalais de Recherches Agricoles–Université Cheikh Anta Diop (UCAD), Département de Biologie Végétale, UCAD, BP 5005 Dakar, Sénégal. ⁵Institute of Botany, Czech Academy of Sciences, Dukelska 135, 379 01 Trebon, Czech Republic. ⁶School of Earth Sciences and Environmental Sustainability, Northern Arizona University, Flagstaff, AZ 86011-5694, USA. ⁷Netherlands Institute of Ecology, Droevendaalsesteeg 10, 6708 PB Wageningen, Netherlands. ⁸TERI-Deakin Nano Biotechnology Centre, Biotechnology and Management of Bioresources Division, TERI, India Habitat Centre, Lodhi Road, New Delhi 110 003, India.

*Corresponding author. E-mail: john.davison@ut.ee (J.D.); mari.moora@ut.ee (M.M.); maarja.opik@ut.ee (M.O.); martin.zobel@ut.ee (M.Z.) †These authors contributed equally to this work.

Age-related mortality explains life history strategies of tropical and temperate songbirds

Thomas E. Martin

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Wing growth drives songbird selection

Nestling birds are particularly vulnerable to predation, providing pressure for individuals to grow and leave the nest as quickly as possible. In contrast to temperate songbirds, tropical birds appear to grow more slowly despite high rates of nest predation. Martin shows that overall rates of growth are similar across this latitudinal gradient, but tropical birds become mobile more rapidly due to faster wing growth. This trajectory is facilitated by higher provisioning of fewer offspring, providing an example of how life history responds to divergent selection pressures.

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ARTICLE TOOLS

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SUPPLEMENTARY MATERIALS

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