Tropical birds live longer than temperate counterparts

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An international research team has found strong evidence that passerine birds near the equator live longer than their higher latitude counterparts.

Their findings, published today in the journal *The Auk: Ornithological Advances*, underscore the pervasiveness of broad latitudinal patterns in avian life history. The article summarizes six years of bird survey results from a tropical forest site near Manaus, at the center of the Amazon basin, and compares the Manaus results with findings from eleven other sites over a latitude span of more than sixty degrees across the Americas.

It has been well known for more than half a century that birds from tropical areas tend to lay fewer eggs per clutch than birds from temperate or higher-latitude regions. This might suggest that tropical bird populations grow slower than populations from higher latitudes, but there is no empirical support for such difference in population growth rates. As a consequence, ornithologists have thought that some other aspect of bird life history must show a latitudinal variation that offsets the clutch size trend.

Adult survival probability, which translates into lifespan, has often been assumed to be the offsetting life history variable. Higher survival rates in tropical regions would offset the smaller clutch size. Nonetheless, there has been scarce evidence to support the idea of high tropical survival. Indeed, arguably the most careful comparison of bird survival rates to date, a 1990 study by James R. Karr and colleagues, found no support for a latitudinal trend and was subtitled "Will the dogma survive?"

An alternative idea is that, in the absence of a latitudinal trend in adult survival, there might be one in juvenile survival rates. Accordingly, a 2011 study led by Corey Tarwater, now at the University of Wyoming, documented exceptionally high juvenile survival in one Central American passerine species and suggested that this could be part of a broader trend. With little variation in adult survival and higher juvenile survival in the tropics, however, one should expect relatively little difference between tropical adult and juvenile survival rates.

The authors of the present study, led by Gonçalo Ferraz from the Federal University of Rio Grande do Sul, Brazil, set out to measure the difference between juvenile and adult survival rates for a set of forty species from their Manaus site, in the Brazilian Amazon two degrees south of the equator. Their first key finding was that mean juvenile survival in the Manaus sample is clearly lower than mean adult survival. Subsequently, they carried out a meta-analysis of the variation of survival with latitude, combining data from 175 species and twelve sites from Peru to Alaska.

"It became clear that, on average, forest passerines tend to live longer in tropical than in temperate regions," says Ferraz. The statistically negative relationship between latitude and survival holds even when the analysis jointly accounts for common ancestry among study species, for the time at which the survival estimates where obtained, and for species migration mode.

The main methodological difficulty of this study, say the authors, was that tropical birds are particularly hard to age. While in high-latitude regions birds have a common and well-delimited breeding season, tropical birds often breed throughout the year whenever conditions are appropriate. As a result, while temperate-zone ornithologists encounter juvenile birds in discrete pulses of similarly aged individuals, tropical ornithologists sample populations that contain all possible ages at the

same time.

The solution was two-fold: in-depth study of age determination in the field and statistical accounting for unknown-age birds. "Aging tropical birds in the field is an exercise on reading plumage molts," says Alejandra Muñoz, a Colombian biologist and first author of the study. Alejandra and her field team aged birds with the increasingly popular Wolfe-Ryder-Pyle (WRP) system. WRP divides the lifetime of any bird into distinguishable molt cycles and uses the cycle information to tell whether birds are in their first or subsequent years of life.

Still, after the best efforts to age birds in the field, a non-negligible number of individuals had to be placed in an "unknown-age" category. "The poor man's solution would be to throw away the unknown-age data," says Marc Kéry, a research scientist at the Swiss Ornithological Institute and co-author of the study. Kéry devised a statistical "mixture-model," which uses the difference between juvenile, unknown-age, and adult survival estimates to estimate the proportion of unknown-age birds that are adults and incorporate their information in the study.

The fact that tropical forest passerines have higher survival rates than their higher-latitude counterparts can help ornithologists understand how the long-held latitudinal trend in clutch size could be maintained without latitudinal differences in population growth rate. The idea of longer-lived tropical birds may no longer be seen as a "dogma." What remains to be understood is the relative importance of survival among other possible offsetting traits and the mechanism by which the observed latitudinal trends evolved.

More information: Alejandra Pizarro Muñoz et al, Age effects on survival of Amazon forest birds and the latitudinal gradient in bird survival, *The Auk* (2018). DOI: 10.1642/AUK-17-91.1

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