

New Guinean passerines have globally small clutch-sizes

Benjamin G. Freeman^{A,B,C} and Nicholas A. Mason^{A,B}

^ADepartment of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14850, USA.

^BCornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

^CCorresponding author. Email: bgf27@cornell.edu

Abstract. Tropical birds have small clutches. The mechanisms responsible for generating this pattern remain debated, and are typically examined by comparing tropical species, with small clutches, to their temperate counterparts, with large clutches. However, variation in clutch-size among tropical regions is seldom considered. We show that New Guinean forest passerines lay markedly smaller clutches ($n = 102$ species; mean \pm s.d. = 1.52 ± 0.48) than other tropical avifaunas. Whereas tropical species commonly lay two-egg clutches, a substantial number of New Guinean passerines appear to solely (38%) or frequently (24%) lay single-egg clutches. We used phylogenetic comparative methods to demonstrate that New Guinean passerines lay significantly smaller clutches than congeneric South-East Asian species. We also show that reductions in clutch-size have occurred multiple times among New Guinean passerines, suggesting phylogenetic constraint does not explain this pattern. Instead, current environmental factors, including high levels of parasitism or predation, may explain why New Guinean passerines lay small clutches. We conclude that variation in clutch-size between tropical regions offers a valuable opportunity to test drivers of this variation, such as parasitism and predation, originally developed within a tropical–temperate framework.

Received 12 November 2013, accepted 21 April 2014, published online 1 August 2014

Introduction

Reproduction is a critical aspect of an organism's life history. In birds, reproductive output depends on clutch-size: within a single reproductive season, individuals maximise their fitness by laying larger clutches. Nevertheless, avian clutch-sizes vary tremendously, both within sympatric species assemblages and among conspecifics, or closely related species, inhabiting different regions (e.g. Lack 1947; Cody 1966; Martin *et al.* 2006; Jetz *et al.* 2008). Geographical patterns in clutch-size have been extensively studied to determine what selective factors induce variation in reproductive output among related species in different environments. Perhaps the strongest geographical trend is the pattern for tropical species to lay small clutches (Lack 1947; Martin *et al.* 2006; Jetz *et al.* 2008). Early fieldworkers supported the hypothesis that small clutch-sizes in tropical birds resulted from food limitation in the tropics (e.g. Skutch 1985), although more recent analyses have focussed on mechanistic links between high rates of predation and reduced clutch-size in tropical birds (Martin *et al.* 2000, 2006; Ghalambor and Martin 2001; Jetz *et al.* 2008; Møller and Liang 2013).

Ornithologists investigating why tropical species lay few eggs generally conduct their work in an explicit tropical *v.* temperate-zone framework. That is, they compare clutch-sizes of tropical species to closely related temperate-zone species. This approach has proved fruitful for investigating mechanisms underlying variation in clutch-size (Martin *et al.* 2000, 2006; Ghalambor and Martin 2001; Møller and Liang 2013) but it is not the sole comparative approach that could be used. Variation in clutch-size between tropical regions offers an independent framework to test

hypotheses generated from latitudinal comparisons. Comparing patterns of clutch-size between environmentally similar tropical regions also avoids the confounding effects of environmental differences (e.g. increasing seasonality in the temperate zone) that influence clutch-size and complicate tropical *v.* temperate-zone comparisons. However, clutch-size distributions are thought to vary little between different tropical regions. For example, although the diverse avifaunas of humid forests in the Neotropics, Afrotropics and South-East Asia have largely independent evolutionary histories, they all average approximately two eggs per clutch (Neotropics: Skutch (1985), Martin *et al.* (2006); East Africa: Mkongewa *et al.* (2013); South-East Asia: T. E. Martin, pers. comm.). Despite this, it remains unclear whether the few studies thus far completed accurately capture clutch-size variation in tropical avian communities and there are no summaries of patterns of clutch-size for many tropical avifaunas.

In particular, little is known about clutch-size patterns in New Guinean birds, although Australian species appear to lay small clutches (Yom-Tov 1987; Jetz *et al.* 2008). New Guinea is home to a diverse and largely endemic avifauna mostly restricted to tropical humid forest (Beehler *et al.* 1986) and therefore offers an additional independently evolved avifauna that can be compared to other tropical regions. Although the breeding biology of New Guinean birds is poorly known, sufficient natural history data exist (e.g. Harrison and Frith 1970) to summarise general patterns of clutch-size patterns in the New Guinean avifauna. We provide such a summary for New Guinean forest passerines, and compare New Guinean clutch-sizes to those of closely related species in tropical South-East Asia.

Materials and methods

We collected data on clutch-sizes of New Guinean forest passerines (hereafter ‘New Guinean passerines’) from volumes of the *Handbook of Birds of the World* (e.g. Boles 2007; Frith and Frith 2009; see Supplementary material Tables S1 and S2 for all sources) or from the global analysis of clutch-size by Jetz *et al.* (2008). We did not include estimates of clutch-size that were identified as possible partial clutches. For species with distributions spanning regions outside New Guinea (e.g. species that also occur in Australia), we used clutch-size data only if it came from studies conducted on New Guinean populations.

Examining variation in phenotypic traits among species requires a phylogeny to account for the shared evolutionary history of the taxa at hand (Felsenstein 1985). We therefore conducted phylogenetic comparative analyses to compare clutch-sizes of New Guinean birds to the reproductive output of related species in tropical South-East Asia. Specifically, we compared clutch-size between species living in New Guinea and congeners inhabiting environmentally similar conditions (e.g. large tropical land masses) in South-East Asia. We identified eight genera that together contain 15 species resident in New Guinea and 23 species in tropical South-East Asia, defined for our purposes to comprise the Thai-Malay Peninsula, the large Sundaic Shelf islands of Sumatra, Borneo and Java, and Sulawesi. We used a posterior set of pruned trees from Jetz *et al.* (2012) in combination with phylogenetic generalised least-squares (PGLS; Martins and Hansen 1997) to quantify differences between New Guinea and non-New Guinea taxa while accounting for evolutionary relatedness among species. This analysis was implemented using the packages nlme (Pinheiro *et al.* 2014) and ape (Paradis *et al.* 2004) in the R programming environment (R Development Core Team 2014). We scaled internal branch lengths according to Pagel’s λ model, which estimates the amount of phylogenetic signal present in the evolutionary history of a given character (Pagel 1999; Blomberg *et al.* 2003). In this model, the λ parameter varies from 0 (no phylogenetic signal or a star phylogeny) to 1 (phylogenetic signal equal to Brownian motion or branch lengths remain unchanged) and therefore provides a convenient measure of evolutionary lability for the trait in question. We log-transformed clutch-size in order to meet the assumption of normally distributed residuals (Freckleton 2009) and averaged the model-fitting results over a set of 100 phylogenies randomly selected from a posterior distribution of trees (Jetz *et al.* 2012) to account for uncertainty in topology and branch lengths. To visualise patterns of clutch-size evolution among South-East Asian and New Guinean congeners, we mapped clutch-size onto a single phylogeny from the posterior distribution of Jetz *et al.* (2012) after transforming branches according to the best-fit value of Pagel’s λ using functions from the phytools package (Revell 2012, 2013).

Results

We obtained information on clutch-size for 102 species of New Guinean forest passerines (Supplementary material Table S1). This represents ~40% of currently recognised New Guinean forest passerines (Gill and Donsker 2013). Although there is no information on clutch-size for most New Guinean forest passerines, information does exist for a broad sample of New Guinean

avian diversity, with clutch-size data available for species from 21 families of New Guinean passerines (Supplementary material Table S1). Clutch-sizes are small in New Guinean passerines (mean \pm s.d. = 1.52 ± 0.48 , see Fig. 1), with a large number of species appearing to solely (38%) or frequently (24%, clutch-size of 1–2) lay single-egg clutches (Fig. 1).

We found that passerines in New Guinea from eight different genera had lower clutch-sizes than congeners in South-East Asia ($\beta = -0.48 \pm 0.10$ s.d., $\lambda = 0.65$, $P = 3.8 \times 10^{-5}$; Fig. 2, Supplementary material Table S2). Moreover, our ancestral state reconstruction revealed that small clutches among New Guinea passerines have evolved multiple times (Fig. 2).

Discussion

The mean clutch-size we report for New Guinean passerines (1.52 eggs per clutch; Fig. 1) is the smallest yet reported for any avifauna, and markedly smaller than the previously reported smallest mean clutch-size for a tropical avifauna of 1.9 eggs per clutch in an Afrotropical bird community (Mkongewa, Newmark *et al.* 2013). Moreover, species laying small clutches (mean clutch-size < 2) are present in nearly all families of New Guinean passerines (Supplementary material Table S1), suggesting small clutches are pervasive in New Guinean passerines. This raises the question of why New Guinean passerines lay such small clutches.

Because most New Guinean passerines are members of radiations endemic to New Guinea or Australasia, the pattern of small clutch-sizes in New Guinea could be a result of either an intrinsic property of New Guinean passerine lineages (phylogenetic niche conservatism of small clutches) or an extrinsic property of the New Guinean environment that selects for small clutches. We first consider the hypothesis that New Guinean passerines may lay small clutches owing to phylogenetic constraint. For example, Australian passerines lay small clutches (Yom-Tov 1987; Jetz *et al.* 2008), a pattern observed in both cooperatively breeding (Cockburn 2003, 2006) and non-cooperative Australian species

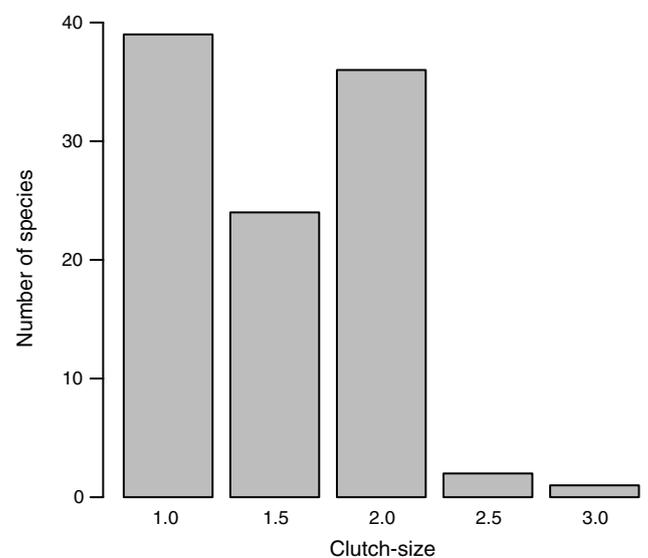


Fig. 1. Histogram of interspecific clutch-size variation in New Guinean forest passerines. Nearly equivalent numbers of species lay clutches of one or two, whereas very few species lay clutches greater than two.

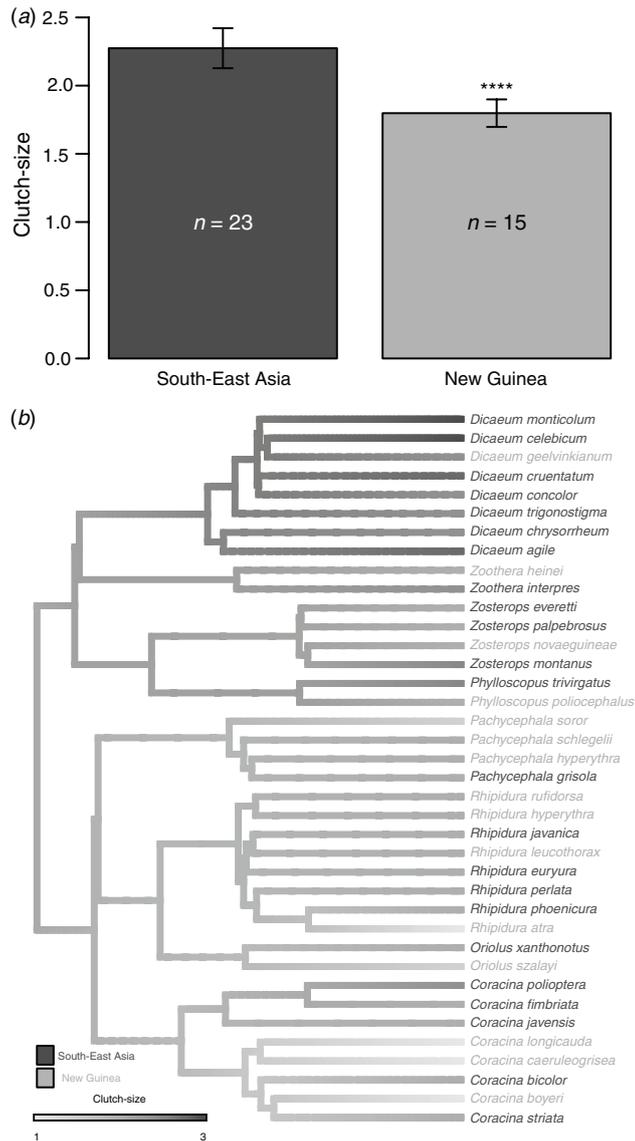


Fig. 2. Phylogenetic comparative analyses using a pruned posterior distribution of phylogenies from Jetz *et al.* (2012) show reduced clutch-sizes in New Guinean passerines ($n = 15$) compared to related taxa in South-East Asia ($n = 23$). (a) The difference in clutch-size between New Guinean (light grey; $n = 15$) and South-East Asian (dark grey; $n = 23$) passerines within a phylogenetic generalised least-squares framework under Pagel's λ model. (b) An ancestral state reconstruction of changes in clutch-size among eight genera of passerines that include species in New Guinea (light-grey labelling) and South-East Asia (dark grey labelling) after rescaling the phylogeny according to Pagel's λ model. The darkness of each branch indicates the reconstructed clutch-size, where darker branches reflect larger clutches.

(Yom-Tov 1987; Green and Cockburn 1999; Magrath *et al.* 2000). This pattern is especially pronounced within the several core families of the Corvoidea (*sensu* Irestedt and Ohlson 2008) that comprise a large portion of the Australian (Yom-Tov 1987) and New Guinean avifauna (Beehler *et al.* 1986). In this view, reduced clutches may have evolved in response to past environmental factors within dominant lineages of New Guinean passer-

ines and these patterns persist in extant species owing to evolutionary constraint.

To evaluate this hypothesis, we conducted phylogenetic comparative analyses of New Guinean passerines and their relatives outside of New Guinea. We found that closely related (congeneric) species have significantly smaller clutches if they inhabit New Guinea and larger clutches if they inhabit environmentally similar conditions in South-East Asia, a distinct tropical region (Fig. 2). We interpret these findings as suggesting that clutch-sizes in New Guinean passerines are reduced principally as a result of environmental factors specific to New Guinea that select for small clutches. Our finding that clutch-sizes are evolutionarily labile within New Guinean passerine lineages agrees with a recent global macroecological analysis that found little phylogenetic constraint on clutch-size (Pienaar *et al.* 2013).

Because phylogenetic constraint does not appear to explain reduced clutch-sizes in New Guinean passerines, we suggest this pattern of small clutch-sizes may result from extrinsic factors of the New Guinean environment, namely unusual selective pressures faced by breeding New Guinean passerines. It is currently not known what these selective pressures might be, as there have been no comprehensive studies of the breeding biology of New Guinean birds. Studies in Neotropical and Asian tropical birds have linked increased nest predation and adult survival to the evolution of smaller clutches (Martin *et al.* 2000, 2006; Ghalambor and Martin 2001; Møller and Liang 2013). Equally, parasites exert strong selection on tropical birds to lay small clutches, as parasite virulence on nesting birds is highest at tropical latitudes (Møller *et al.* 2009). These studies suggest that New Guinean passerine clutch-sizes may be globally small in part owing to higher rates of predation and parasitism compared to other tropical regions. There are indirect suggestions that New Guinean passerines may experience intense predation and parasitism. For example, toxic plumage has evolved in multiple independent lineages of New Guinean passerines, all of which lay small clutches (Blue-capped Ibrit (*Ibrita kowaldi*), clutch 1 egg; and Black (*Pitohui nigrescens*) and Hooded (*P. dichrous*) Pitohuis, clutch 1–2; Dumbacher *et al.* 1992, 2008; Supplementary material Table S1). Most New Guinean lineages that lay single-egg clutches do not exhibit toxic plumage and we do not suggest a direct link between clutch-size and toxic plumage. Nevertheless, the fact that toxic plumage has evolved only in New Guinean passerines despite the pantropical distribution of the toxin's putative source, melyrid beetles (Dumbacher *et al.* 2004), is consistent with the hypothesis that New Guinean birds experience globally unique predation or parasitism pressure.

Finally, we consider the limitations of our data. As is generally true for tropical regions (Jetz *et al.* 2008), breeding biology is poorly studied in New Guinea. This raises the possibility that current data on New Guinean passerine clutch-size are insufficient to draw general conclusions. Although data on clutch-size in New Guinean passerines is sparse, our database includes clutch-size information for more than 100 species in 21 families (Supplementary material Table S1). We used standard reference volumes (e.g. *Handbook of Birds of the World*) to compile our data. We were thus unable to weight estimates of clutch-size by sample size, possibly influencing the results of our comparative analyses (Garamszegi and Møller 2010). We consider our methodology reasonable, given that estimates of clutch-size were

based on multiple complete clutches for all but six species. Although future discoveries will undoubtedly improve our current knowledge of clutch-size in New Guinean passerines, additional data is unlikely to change substantially the conclusion that New Guinean passerines lay globally small clutch-sizes.

In conclusion, the current literature suggests that clutch-sizes in New Guinean birds are the smallest of any region – tropical or temperate – in the world. Phylogenetic constraint in the evolution of clutch-size within New Guinean passerines appears to be weak or non-existent, outweighed by the influence of New Guinean environmental conditions. Because New Guinean passerines inhabit an abiotic environment similar to that of other tropical regions where clutch-sizes are larger, we suggest that biotic factors specific to New Guinea have driven the evolution of globally small clutch-sizes within New Guinean passerines. In particular, future research should test the hypothesis that rates of nest predation and parasitism and adult survival, both linked to reduced clutch-sizes in tropical birds in other geographical regions, are especially high in New Guinean birds.

Supplementary material

The Supplementary material contains clutch-size estimates for species analysed in this manuscript. This is available from the journal online (see http://www.publish.csiro.au/?act=view_file&file_id=MU14023_AC.pdf).

Acknowledgements

We thank T. Martin and his lab group for drawing our attention to the atypical patterns of clutch-size exhibited by New Guinean birds. Comments from A. C. Freeman, E. Miller and two anonymous reviewers improved this manuscript. Field studies of New Guinean avian ecology by B. G. Freeman were supported by grants from the National Geographic Society (Washington, DC) (CRE grant 9117–12) and the Athena Fund of the Cornell Laboratory of Ornithology (Ithaca, NY). This material is based upon work supported by the National Science Foundation Graduate Research Fellowship under Grant No. 2011083591 to B. G. Freeman.

References

- Beehler, B. M., Pratt, T. K., and Zimmerman, D. A. (1986). 'Birds of New Guinea.' (Princeton University Press: Princeton, NJ.)
- Blomberg, S. P., Garland, T., and Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**(4), 717–745. doi:10.1111/j.0014-3820.2003.tb00285.x
- Boles, W. E. (2007). Family Pachycephalidae (Whistlers). In 'Handbook of the Birds of the World. Vol 12: Picathartes to Tits and Chickadees'. (Eds J. del Hoyo, A. Elliott and D. A. Christie.) pp. 374–437. (Lynx Edicions: Barcelona.)
- Cockburn, A. (2003). Cooperative breeding in oscine passerines: does sociality inhibit speciation? *Proceedings of the Royal Society of London – B. Biological Sciences* **270**(1530), 2207–2214. doi:10.1098/rspb.2003.2503
- Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London – B. Biological Sciences* **273**(1592), 1375–1383. doi:10.1098/rspb.2005.3458
- Cody, M. L. (1966). A general theory of clutch size. *Evolution* **20**, 174–184. doi:10.2307/2406571
- Dumbacher, J. P., Beehler, B. M., Spande, T. F., Garraffo, H. M., and Daly, J. W. (1992). Homobatrachotoxin in the genus *Pitohui*: chemical defense in birds? *Science* **258**(5083), 799–801. doi:10.1126/science.1439786
- Dumbacher, J. P., Wako, A., Derrickson, S. R., Samuelson, A., Spande, T. F., and Daly, J. W. (2004). Melyrid beetles (*Choresine*): a putative source for the batrachotoxin alkaloids found in poison-dart frogs and toxic passerine birds. *Proceedings of the National Academy of Sciences of the United States of America* **101**(45), 15857–15860. doi:10.1073/pnas.0407197101
- Dumbacher, J. P., Deiner, K., Thompson, L., and Fleischer, R. C. (2008). Phylogeny of the avian genus *Pitohui* and the evolution of toxicity in birds. *Molecular Phylogenetics and Evolution* **49**(3), 774–781. doi:10.1016/j.ympev.2008.09.018
- Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist* **125**, 1–15. doi:10.1086/284325
- Freckleton, R. (2009). The seven deadly sins of comparative analysis. *Journal of Evolutionary Biology* **22**(7), 1367–1375. doi:10.1111/j.1420-9101.2009.01757.x
- Frith, C., and Frith, D. (2009). Family Paradisaeidae (Birds of Paradise). In 'Handbook of the Birds of the World. Vol. 14: Bush-shrikes to Old World Sparrows'. (Eds J. del Hoyo, A. Elliott and D. A. Christie.) pp. 404–493. (Lynx Edicions: Barcelona.)
- Garamszegi, L. Z., and Møller, A. P. (2010). Effects of sample size and intraspecific variation in phylogenetic comparative studies: a meta-analytic review. *Biological Reviews of the Cambridge Philosophical Society* **85**(4), 797–805.
- Ghalambor, C. K., and Martin, T. E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science* **292**(5516), 494–497. doi:10.1126/science.1059379
- Gill, F., and Donsker, D. (Eds) (2013). 'IOC World Bird List (v 3.4).' Available at <http://www.worldbirdnames.org> [Accessed 5 June 2013].
- Green, D. J., and Cockburn, A. (1999). Life history and demography of an uncooperative Australian passerine, the Brown Thornbill. *Australian Journal of Zoology* **47**(6), 633–649. doi:10.1071/ZO99052
- Harrison, C., and Frith, C. (1970). Nests and eggs of some New Guinea birds. *Emu* **70**(4), 173–178. doi:10.1071/MU970173
- Irestedt, M., and Ohlson, J. I. (2008). The division of the major songbird radiation into *Passerida* and 'core *Corvoidea*' (Aves: Passeriformes) – the species tree vs. gene trees. *Zoologica Scripta* **37**(3), 305–313. doi:10.1111/j.1463-6409.2007.00321.x
- Jetz, W., Sekercioglu, C. H., and Bohning-Gaese, K. (2008). The worldwide variation in avian clutch size across species and space. *PLoS Biology* **6**(12), e303. doi:10.1371/journal.pbio.0060303
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., and Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* **491**(7424), 444–448. doi:10.1038/nature11631
- Lack, D. (1947). The significance of clutch-size. *Ibis* **89**(2), 302–352. doi:10.1111/j.1474-919X.1947.tb04155.x
- Magrath, R. D., Leedman, A. W., Gardner, J. L., Giannasca, A., Nathan, A. C., Yezerinac, S. M., and Nicholls, J. A. (2000). Life in the slow lane: reproductive life history of the White-browed Scrubwren, an Australian endemic. *Auk* **117**(2), 479–489. doi:10.1642/0004-8038(2000)117[0479:LITSLR]2.0.CO;2
- Martin, T. E., Martin, P., Olson, C., Heidinger, B., and Fontaine, J. (2000). Parental care and clutch sizes in North and South American birds. *Science* **287**(5457), 1482–1485. doi:10.1126/science.287.5457.1482
- Martin, T. E., Bassar, R., Bassar, S., Fontaine, J., Lloyd, P., Mathewson, H., Niklison, A., and Chalfoun, A. (2006). Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. *Evolution* **60**(2), 390–398. doi:10.1111/j.0014-3820.2006.tb01115.x
- Martins, E. P., and Hansen, T. F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* **149**, 646–667. doi:10.1086/286013
- Mkongewa, V. J., Newmark, W. D., and Stanley, T. R. (2013). Breeding biology of an Afrotropical forest understory bird community in north-

- eastern Tanzania. *Wilson Journal of Ornithology* **125**(2), 260–267. doi:[10.1676/12-138.1](https://doi.org/10.1676/12-138.1)
- Møller, A. P., and Liang, W. (2013). Tropical birds take small risks. *Behavioral Ecology* **24**(1), 267–272. doi:[10.1093/beheco/ars163](https://doi.org/10.1093/beheco/ars163)
- Møller, A. P., Arriero, E., Lobato, E., and Merino, S. (2009). A meta-analysis of parasite virulence in nestling birds. *Biological Reviews of the Cambridge Philosophical Society* **84**(4), 567–588. doi:[10.1111/j.1469-185X.2009.00087.x](https://doi.org/10.1111/j.1469-185X.2009.00087.x)
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* **401**(6756), 877–884. doi:[10.1038/44766](https://doi.org/10.1038/44766)
- Paradis, E., Claude, J., and Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**(2), 289–290. doi:[10.1093/bioinformatics/btg412](https://doi.org/10.1093/bioinformatics/btg412)
- Pienaar, J., Ilany, A., Geffen, E., and Yom-Tov, Y. (2013). Macroevolution of life-history traits in passerine birds: adaptation and phylogenetic inertia. *Ecology Letters* **16**(5), 571–576. doi:[10.1111/ele.12077](https://doi.org/10.1111/ele.12077)
- Pinheiro, J., Bates, D., DebRoy, S. S., Sarkar, D., and R Development Core Team (2014). *Nlme: linear and nonlinear mixed effects models*. R Package, ver. 3.1-117.
- R Development Core Team (2014). *R: a language and environment for statistical computing*. (R Foundation for Statistical Computing: Vienna, Austria.)
- Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**(2), 217–223. doi:[10.1111/j.2041-210X.2011.00169.x](https://doi.org/10.1111/j.2041-210X.2011.00169.x)
- Revell, L. J. (2013). Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution* **4**, 754–759. doi:[10.1111/2041-210X.12066](https://doi.org/10.1111/2041-210X.12066)
- Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Ornithological Monographs* **36**, 575–594. doi:[10.2307/40168306](https://doi.org/10.2307/40168306)
- Yom-Tov, Y. (1987). The reproductive rates of Australian passerines. *Wildlife Research* **14**(3), 319–330. doi:[10.1071/WR9870319](https://doi.org/10.1071/WR9870319)