New Guinean passerines have globally small clutch-sizes

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

\textsuperscript{A}Department of Ecology and Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14850, USA. \textsuperscript{B}Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA. \textsuperscript{C}Corresponding 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 larger 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 \(\pm\) 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.

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: Mkonge\textsuperscript{a}wa 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.
New Guinean passerines lay small clutches

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 Sundaric 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 ± 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 (β = −0.48 ± 0.10 s.d., λ = 0.65, P = 3.8 × 10⁻⁶; 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 (Mkonge圣诞, 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.](image)
The phrase "core families of the Corvoidea (Fig. 2)" is not clearly visible in the image. It is likely that the phrase is referring to a figure that is not visible in the provided image. The text suggests that the authors are examining the evolution of clutch sizes in New Guinean passerines, comparing them to South-East Asia, and discussing the implications of this comparison for understanding evolutionary patterns.

They conclude by stating that the reduced clutch sizes in New Guinean passerines may be a result of environmental factors specific to New Guinea, such as unique predation or parasitism pressures, or other evolutionary pressures unique to that region.

The authors also mention the use of phylogenetic comparative methods to analyze clutch sizes and suggest that this approach can provide insights into the evolutionary history of bird species in different regions.
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 Athen 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


