

Temporal Environmental Variability Drives the Evolution of Cooperative Breeding in Birds

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Summary

Many vertebrates breed in cooperative groups in which more than two members provide care for young [1, 2]. Studies of cooperative breeding behavior within species have long highlighted the importance of environmental factors in mediating the paradox of why some such individuals delay independent breeding to help raise the offspring of others [3, 4]. In contrast, studies involving comparisons among species have not shown a similarly clear evolutionary-scale relationship between the interspecific incidence of cooperative breeding and any environmental factors [5–11]. Here, we use a phylogenetically controlled comparative analysis of a complete, socially diverse group of birds—45 species of African starlings—to show that cooperative breeding is positively associated with living in semiarid savanna habitats and with temporal variability in rainfall. Savanna habitats are not only highly seasonal, but also temporally variable and unpredictable, and this temporal variability directly influences individual reproductive decisions in starlings and helps explain interspecific patterns of sociality. Cooperative breeding is likely to be adaptive in temporally variable environments because it allows for both reproduction in harsh years and sustained breeding during benign years [12]. This “temporal variability” hypothesis might help explain the phylogenetic and geographic concentrations of cooperatively breeding vertebrates in savanna-like habitats and other temporally variable environments worldwide.

Results and Discussion

Although the first observations of cooperative breeding in birds were made in New World tropical forests [13], most avian cooperative breeders are found in semiarid tropical and subtropical environments, particularly in sub-Saharan Africa and Australia [6–8, 11, 14]. Whereas these broad-scale patterns suggest that basic features of the environment select for cooperative breeding behavior, few studies have shown a strong relationship

between the interspecific incidence of cooperative breeding and environmental variables [5–11]. Although cooperative species often occur in semiarid woodland and savanna habitats, rather than rainforests or deserts [6–8, 14], there has been no consensus on which environmental variables best explain these patterns [15]; cooperative breeders have been suggested to occur disproportionately in both seasonal [6] and aseasonal environments [8], as well as in both stable [10, 16] and unstable environments [11]. Additionally, most studies of these associations have been confounded by the roles that life history and phylogeny might play in the evolution of cooperative breeding, or by their deep taxonomic level of comparison [15, 17]. Cooperative breeding appears to be ancestral in some, but not all, groups of birds [15, 17], making it especially important to control for phylogenetic effects in studies that compare recently evolved behavioral differences among lineages that have diverged in their social systems.

Here, we present a complete, species-level molecular phylogeny of a speciose and socially diverse avian group, the African starlings, and use it to determine the role that environmental factors have played in the evolution and maintenance of cooperative breeding. We then employ long-term precipitation data from across Africa to characterize the degree of seasonality and predictability of different habitats and directly relate temporal patterns of rainfall to the incidence of sociality in starlings to elucidate a possible mechanism favoring the evolution and maintenance of cooperative breeding in this group.

The species in the African radiation of the Sturnidae inhabit nearly the full range of habitats on the continent, from arid deserts, to semiarid mixed tree-grass savanna woodlands, to tropical moist forests (Table S1 in the Supplemental Data available online) [18, 19]. The social systems of these species range in complexity from simple noncooperative monogamous pairs, to small, singular cooperatively breeding groups with one breeding pair and few helpers, to large, complex, plural cooperatively breeding groups with multiple breeding pairs and many helpers [18, 19]. In total, nearly 40% of the starlings endemic to Africa are cooperative breeders.

We built a molecular phylogeny including all 45 African starlings belonging to a clade that radiated almost exclusively in Africa and its satellite islands (Figure 1) [20]. This tree was reconstructed with Bayesian likelihood methods applied to extensive mitochondrial and nuclear intron sequences, and its high topological resolution provides a robust framework for testing for potential associations among social systems and environmental factors. For each species, we classified its primary social system (cooperative versus noncooperative) and preferred habitat type (savanna versus nonsavanna). These characters were mapped onto the tree and analyzed with a phylogenetically controlled comparative analysis.

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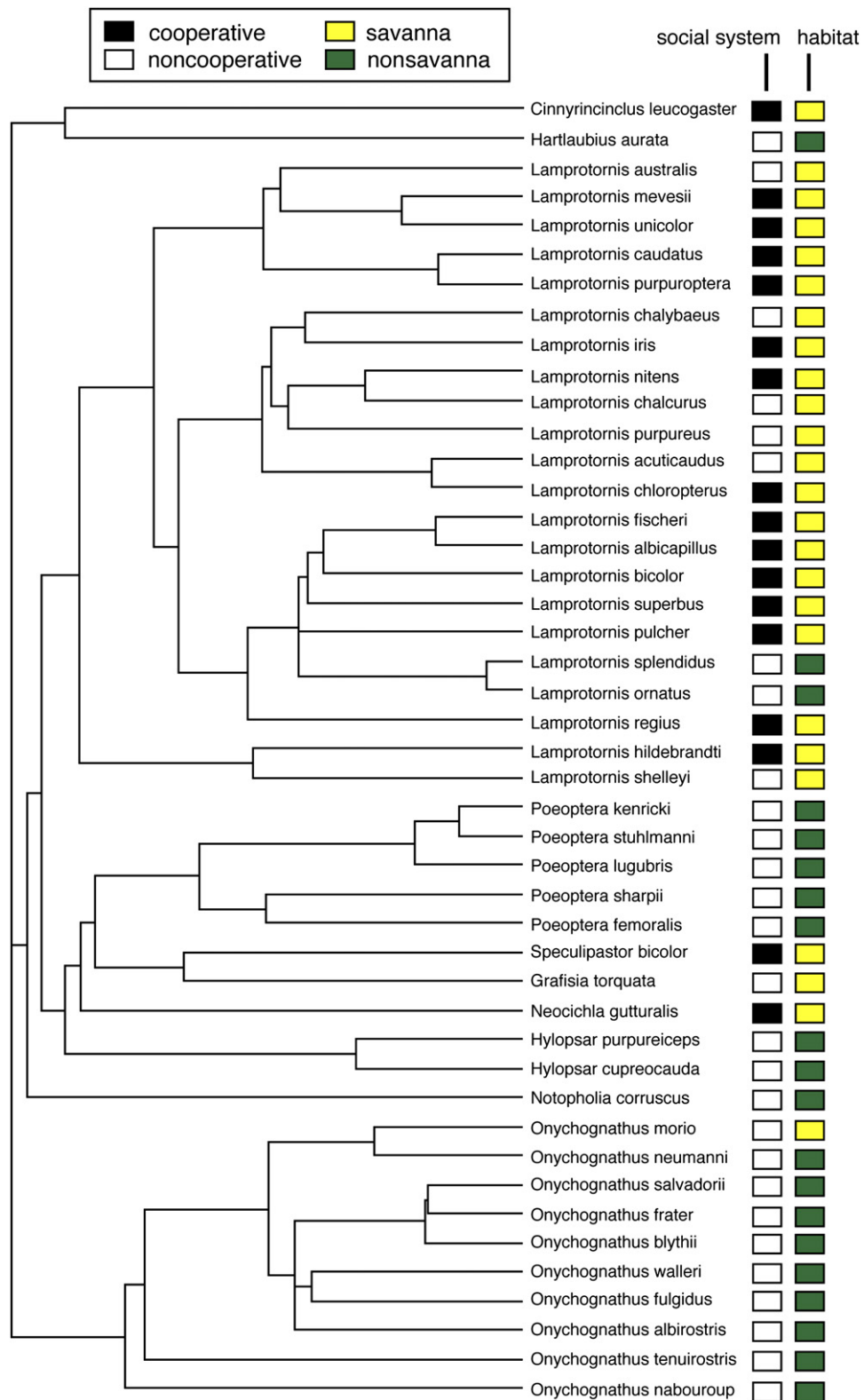


Figure 1. Molecular Phylogeny of African Starlings and Their Social Behavior in Relation to Environmental Factors

This ultrametric Bayesian MCMC topology is based on the combined analysis of mitochondrial and nuclear intron sequences. The social and environmental characters used in comparative analyses are indicated to the right of each terminal species. All characters are discrete and were treated as binary; a key is given above the tree. Social systems were divided into cooperative and noncooperative. Habitats were divided into savanna and nonsavanna.

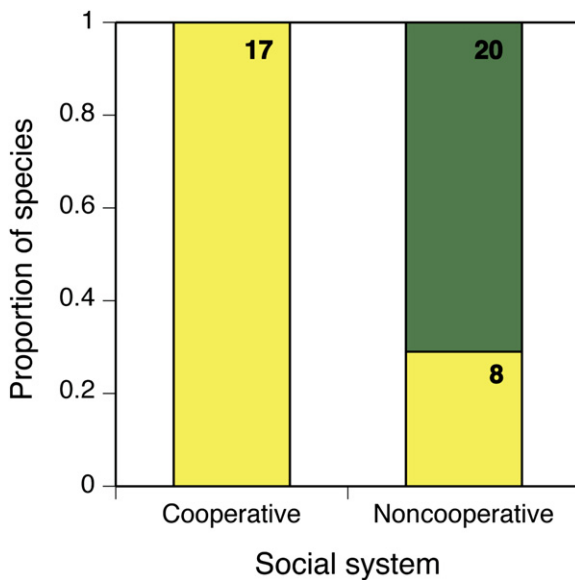


Figure 2. Proportions of Cooperatively Breeding African Starlings in Different Habitats

Cooperative breeding is more prevalent in species that occupy savannas (yellow bars) than it is in those found in nonsavanna habitats (green bars). All 45 African starlings were used in the analysis, and the numbers of species in each group are indicated in the corner of each bar.

We found that cooperatively breeding species were more prevalent in savanna habitats than in nonsavanna habitats (likelihood ratio = 17.9, $p < 0.0001$; Figure 2). Although nonsavanna habitats included both deserts and forests, only four species (all in the genus *Onychognathus*) live in deserts, and none are cooperative breeders. The absence of cooperative breeders in deserts is presumably due to the very low mean annual precipitation (MAP), which might preclude permanent year-round territories, a prerequisite for most obligate cooperative breeders [6, 16]. Ultimately, explaining why cooperatively breeding African starlings are most prevalent in savannas requires understanding the unique ecology of these semiarid ecosystems.

In addition to having a relatively low MAP, semiarid savanna ecosystems are characterized by a high temporal variability of precipitation events [21]. Although most African savannas receive seasonal rainfall generated by the monsoons, rainfall is erratic in time and space [22]. Whereas landscape heterogeneity, or spatial environmental variation, has been featured in many explanations for the evolution of cooperative breeding [1, 3, 4, 23–26], there has been much less emphasis on the role of temporal, or year-to-year, environmental variation in the evolution of sociality [3, 12]. Temporal variability in rainfall directly influences many of the reproductive decisions of the cooperatively breeding birds and mammals in African savannas [6, 12, 27], and probably explains why cooperative breeding in starlings is more common in savannas than it is in more environmentally predictable and stable forests. If cooperative breeding is an adaptation that allows these species to buffer the effects of unpredictable rainfall and food availability, then cooperative breeders should be found in those

areas with the most variable and unpredictable rainfall patterns.

We examined environmental variability in two ways by using the long-term precipitation data spanning as much as 147 years from 2,171 sites across 47 African countries [28]. First, we measured the variation in MAP by calculating coefficients of variation (CV). Second, we estimated Colwell's measure of predictability for temporal patterns, which is the sum of constancy, a measure of uniformity across time intervals, and contingency, a measure of the degree of change from season to season [29]. Thus, constancy measures year-to-year stochastic variations in temporal patterns (i.e., temporal variability), whereas contingency measures to what degree a seasonal pattern is repeated within each year (i.e., seasonality).

We found that precipitation overall was more variable in drier areas than it was in wetter areas ($F_{1,2169} = 6388$, $p < 0.0001$, $r = 0.87$; Figure 3A). Deserts had a higher variation in MAP than did savannas, which in turn had a higher variation than did forests ($F_{2,269} = 914$, $p < 0.0001$; all contrasts, $p < 0.0001$; Figure 3B). Although variation in MAP declined linearly with increasing MAP, predictability showed a nonlinear relationship with MAP ($F_{2,2168} = 192$, $p < 0.0001$, $r = 0.39$; Figure 3C), such that savannas were significantly more unpredictable than were both deserts and forests ($F_{2,270} = 79.6$, $p < 0.0001$; all contrasts, $p < 0.0001$; Figure 3F). There was a similar nonlinear relationship between constancy and MAP ($F_{2,2168} = 927$, $p < 0.0001$, $r = 0.68$; Figure 3D), suggesting that the pattern in unpredictability was driven primarily by differences in temporal variability (constancy) between habitats; savannas showed a higher year-to-year stochastic variability (i.e., lower constancy) than did both deserts and forests ($F_{2,253} = 169$, $p < 0.0001$; all contrasts, $p < 0.0001$; Figure 3F). Additionally, there was a linear relationship between contingency and MAP ($F_{1,2169} = 615$, $p < 0.0001$, $r = 0.47$; Figure 3E), showing that rainfall patterns in savannas were highly seasonal. Although contingency in savannas was significantly higher than it was in deserts but lower than it was in forests ($F_{2,343} = 608$, $p < 0.0001$; all contrasts, $p < 0.0001$; Figure 3F), the degree of seasonality in savannas was much more similar to that in forests than in deserts. These results demonstrate that semiarid savanna woodlands are extremely unpredictable environments characterized by high temporal variability and high seasonality.

Because differences in predictability among habitats—particularly between savannas and forests—were mainly driven by differences in temporal variability, we used a comparative analysis on phylogenetically independent contrasts to test the hypothesis that sociality is directly related to the degree of temporal variability in precipitation. This test was designed to determine whether there is a direct link between temporal variability and the incidence of sociality, thereby testing for a mechanism that favors the evolution and maintenance of cooperation in African starlings. We georeferenced point localities from published comprehensive species-range maps [30] and then used geographic information systems (GIS) to estimate precipitation variables for each species. As predicted, cooperatively breeding starlings were more prevalent in areas with high temporal

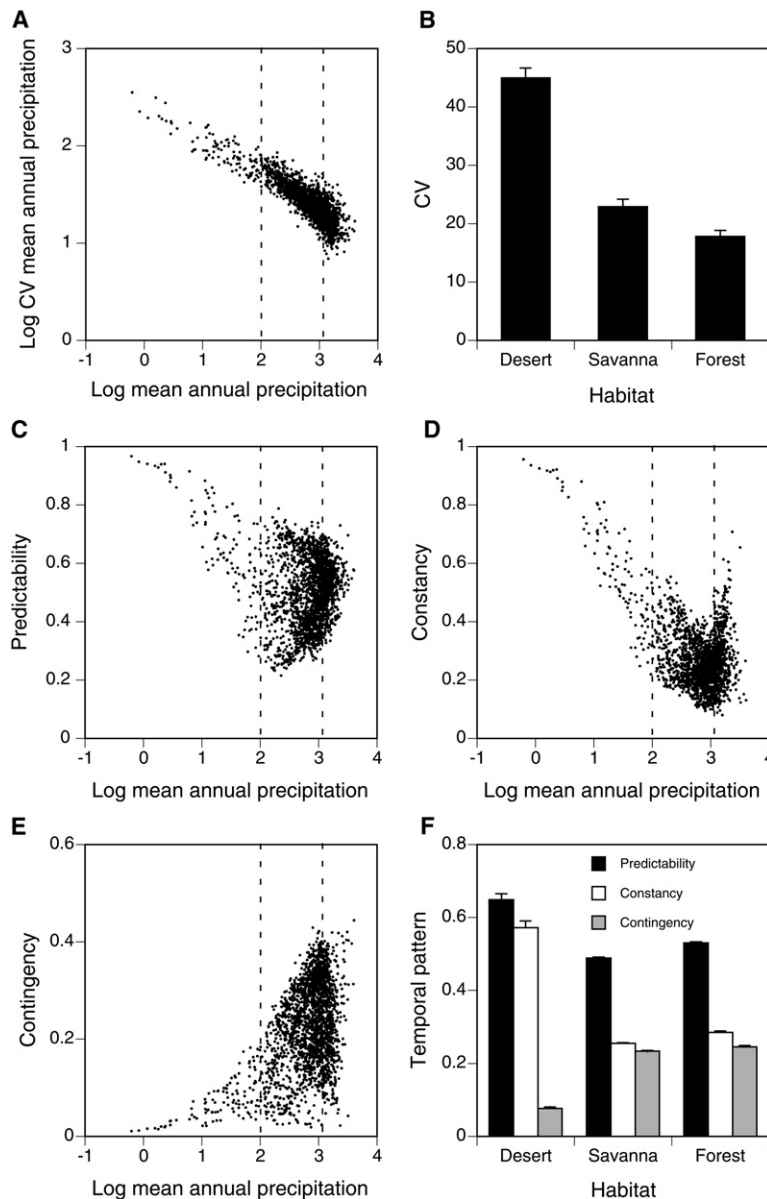


Figure 3. Temporal Patterns of Variation in African Precipitation

(A) Correlation between MAP and variation in MAP. The vertical dotted lines indicate the boundaries between desert and savanna, as well as between savanna and forest. The coefficient of variation (CV) in MAP is negatively correlated with MAP.

(B) Variation in MAP in different habitats. The mean \pm standard error (SE) values are shown. Deserts have higher variation in MAP than do savannas, which have higher variation in MAP than do forests.

(C) Correlation between MAP and predictability. There is a nonlinear relationship such that savannas are more unpredictable than are either deserts or forests. Predictability has two components: constancy (a measure of temporal variability) and contingency (a measure of seasonality).

(D) Correlation between MAP and constancy. There is a nonlinear relationship such that savannas are more temporally variable than are either deserts or forests.

(E) Correlation between MAP and contingency. There is a linear relationship of increasing seasonality from deserts to forests.

(F) Comparisons of predictability, constancy, and contingency among habitats. The mean \pm SE values are shown. Savannas are less predictable and have higher temporal variability than deserts and forests. Deserts are less seasonal than are savannas, which are nearly as seasonal as are forests.

variability (i.e., low constancy), and noncooperatively breeding species were more common in areas with low temporal variability (i.e., high constancy) ($F_{1,10} = 6.07$, $p = 0.035$). Despite the similar patterns of predictability and constancy among habitats (Figure 3), there was no relationship between predictability and the incidence of sociality in starlings ($F_{1,10} = 0.34$, $p = 0.57$), presumably because most habitats occupied by starlings were highly seasonal (i.e., high contingency).

Our results demonstrate that cooperative breeding within a large, socially diverse group of birds is associated with temporally variable environments. That is, temporal variability in annual precipitation appears to be a mechanism that favors the evolution and maintenance of cooperation in African starlings. Cooperative breeding is likely to be an adaptation to temporally variable, but seasonal, environments because it allows for successful reproduction in harsh years when low rainfall

and food availability directly influence reproductive decisions [3, 12, 27], as well as for sustained breeding during benign years [11]. Most starlings are omnivorous, but they prefer insects, particularly during the breeding season [18, 19], when seasonal rainfall leads to an increase in insect abundance [22]. Long-term studies of three locally sympatric species of African *Lamprotornis* starlings have shown that the most-social species (an obligate cooperative breeder, *L. superbus*) (1) breeds in years when the less-social species (one occasional cooperative breeder, *L. hildebrandti*, and one noncooperative breeder, *L. chalybaeus*) do not, and (2) does so for significantly longer (and by laying more clutches) than do the two less-social species (D.R.R. unpublished data 2001–2007). It is not clear why noncooperative starlings living in temporally stable forest environments, as well as the few noncooperative species living in temporally variable savanna environments, are not also

selected to receive similar reproductive benefits via cooperation; presumably either the costs of cooperation or the benefits of independent breeding outweigh the reproductive benefits of cooperation for these species [16].

In a broader geographic and taxonomic context, the relationship between cooperative breeding and environmental variability in African starlings might help explain the disproportionately high incidence of cooperatively breeding birds in Africa and Australia [6–8, 14], as well as in many of the semiarid Mediterranean and savanna habitats throughout the world that exhibit similarly temporally variable rainfall patterns. Moreover, this temporal-variability hypothesis might also explain the high incidence of cooperative breeding in many social carnivores and other mammals found in savannas throughout Africa and worldwide [31]. Although temperature has been suggested to influence the incidence of avian cooperative breeding at a deep taxonomic scale [17], that pattern was driven mainly by large-scale temperature differences between temperate and tropical regions [10]. In tropical environments, where cooperative breeders are much more common, variation in rainfall is likely to be more important than temperature in shaping the breeding life histories of avian species [22] because rainfall mediates food availability, which in turn greatly influences the timing of reproduction and the ability of birds to maintain year-round territories [6, 16]. Because many normally noncooperatively breeding birds throughout the northern hemisphere and elsewhere have been observed to exhibit occasional cooperative behavior [32], understanding how species behave in naturally variable environments will be important for predicting how these typically noncooperative breeders might adopt alternative social systems under conditions of increasing environmental variability [33, 34].

Experimental Procedures

Phylogeny Reconstruction

We included all 45 Sturnidae species that are of African origin and endemic to mainland Africa and its satellite islands [20]. We excluded the two *Buphagus* oxpeckers because their lineage is basal to both Old World Sturnidae and the related New World Mimidae, as well as *Creatophora cinera*, because it is the sole African species in an otherwise Eurasian starling clade [20]. Two species (*Saroglossa spiloptera* and *Onychognathus tristranii*) in the African clade considered here were also not included in the analysis because they are endemic to Asia [20].

A detailed description of phylogenetic reconstruction methods, samples, and markers was published previously [20]. Phylogenetic analyses were run again for this study to add the final African starling species (*Onychognathus neumani*) that was not available previously. In brief, we used Bayesian Markov chain Monte Carlo (MCMC) methods as implemented in MrBayes v3.1 [35] and maximum parsimony as implemented in Paup* v4.0b10 [36] to reconstruct the phylogeny from a DNA-sequence character matrix (4108 bp mtDNA + 2974 bp from 4 intron loci from most taxa; or 1041 bp mtDNA from samples derived from older museum skins).

Characters

Because the relevant comparative analysis algorithms can employ only binary characters [37, 38], each species of starling was assigned one of two states for social and environmental characters (Figure 1, Table S1). Species were classified as “cooperative” or “noncooperative” through the use of published species accounts [18, 19] and direct observations. Although information about the

social behavior of some species is limited, reports of the number of birds attending nestlings—or our observations—are available for all but two species (*Poepotera kenricki* and *Hartlaubius aurata*), which we classified as noncooperative [18, 19]. The preferred habitat of each species was determined through the use of published accounts [18, 19, 30] and habitat classification systems for Africa [39, 40]. Species were classified into those living in “savanna,” or mixed tree-grass savanna woodlands characterized by medium to low MAP, or “nonsavanna,” or those characterized by either high (forest) or low (desert) MAP.

Precipitation

Long-term precipitation data were compiled from 2,171 sites across 47 African countries from the National Oceanic and Atmospheric Administration (NOAA) Global Historical Climate Network (GHCN) [28]. MAP ranged from less than 1 mm to more than 4000 mm. Each site was classified into habitat types by levels of MAP: desert, less than 100 mm; savanna, 100–1200 mm; and forest, more than 1200 mm [39]. Only sites with at least ten years of data from all 12 months (mean = 47.5 yrs, range = 10–147 years) were included. All precipitation data were log transformed. Predictability, constancy, and contingency were calculated after binning data into logarithmic classes [29]. Correlations were used to compare climatic data to MAP, and Welch analysis of variance (ANOVA) models, and independent contrasts on least square means were then used to compare climatic data in different habitats.

Mean levels of temporal unpredictability and variability were calculated for each species by the georeferencing of point localities where museum specimens have been collected (mean = 29.5 localities per species, range = 2–126 localities per species) from the maps given in [30] with ArcMap v9.2. A buffer with a diameter of 0.5° latitude was added to each point locality, and GIS was used for determining the GHCN precipitation stations within the vicinity of each locality. Because no GHCN precipitation stations were within the 0.5° buffer of any point localities for *Grafisia torquata*, a 1.0° buffer was used for this one species. Mean predictability and constancy values were calculated for each species from all GHCN stations within its buffer regions. *Onychognathus frater*, which is endemic to the island of Socotra, was excluded from the analysis because there are no GHCN stations on that island. *Hartlaubius aurata*, which is endemic to the island of Madagascar, was also excluded because there are no directly equivalent point-locality data for this species.

Comparative Analyses

To examine the relationship between habitat and the incidence of sociality, we used Pagel’s discrete algorithms [37] in the program Mesquite v1.12 [41]. This analysis uses a continuous-time Markov model and allows for tests of correlated evolution as well as the order and direction of evolution for binary traits [37, 38]. Models of evolution are fit to the data and phylogeny with maximum likelihood and described by the log likelihood of the model. Correlated evolution is detected by comparing a model in which two traits are allowed to evolve independently with one in which they are set to coevolve. The transition rates for the traits were treated as identical, in a one-parameter model in which the forward transition (α) was equal to the backward transition (β). This test compares the log likelihoods of the model of independent evolution (H_0) to those of the model of dependent evolution in which the traits are linked (H_1). Monte Carlo simulations of the independent and dependent models were run 10,000 times, and the p value was reported for a critical value of $\alpha = 0.05$.

To examine the relationship between temporal variability and the incidence of sociality, we used CAIC v2.6 [42] to conduct comparative analyses on phylogenetically independent contrasts from the measures of predictability and constancy. We employed the BRUNCH algorithm with the binary discrete characters for social system (cooperative versus noncooperative). CAIC performs a regression on the contrasts and reports an F ratio and a p value with the appropriate degrees of freedom for the number of independent contrasts calculated from the phylogeny; there were 11 contrasts calculated from our phylogeny. Separate analyses were run for predictability and constancy because the two variables were correlated ($F_{1,9} = 7.92$, $p = 0.02$, $r = 0.68$).

Supplemental Data

One Table is available at <http://www.current-biology.com/cgi/content/full/17/16/1414/DC1/>.

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