Original Article

Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding

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Cooperative breeding occurs in several major animal phyla, predominantly in arthropods and chordates. A number of comparative analyses have focused on understanding the evolution of cooperative breeding, yielding mixed, inconclusive, and often phyla-specific findings. We argue that much of this ambiguity results from an erroneous classification of social systems into noncooperatively and cooperatively breeding species. The shortcomings of this assumption are apparent among birds where noncooperative species constitute a heterogeneous group: some species are clearly non–family living, with offspring dispersing at or shortly after nutritional independency, whereas other species form persistent family groups through offspring delaying their dispersal substantially beyond independency. Here, we propose an objective, life history–based criterion classifying noncooperative bird species into non–family living and family living species. We demonstrate that by using the family time (the time offspring remain with its parent/s beyond independence) and body size–scaled reproductive investment, we are able to differentiate 2 groups with contrasting life histories. Our classification matches seasonal environmental variation experienced by different species: family living species postpone dispersal beyond the onset of less favorable autumn conditions. We discuss the consequences of this new social system classification for evolutionary and ecological research, potentially allowing solutions to some of the most intriguing riddles in the evolutionary history of birds—and cooperative behavior itself.

Key words: **comparative study, cooperation, dispersal, family breeding, life history, parental care, social system.**

INTRODUCTION

Understanding cooperation is fundamental to evolutionary biology, and this question was already seen by Darwin as a great challenge to his theory of natural selection (Darwin 1859). Hamilton's theory of kin selection (Hamilton 1964) resolved the apparent altruism of cooperation among related individuals and provided us with a framework to study the evolution of cooperation in kin groups and, particularly, its most interesting case—cooperative breeding. In many birds and mammals that breed cooperatively, young from previous broods remain with their parents beyond independence and help to raise younger siblings (Hatchwell 2009) although nonkin individuals can also engage in cooperative breeding (Riehl 2013).

Given the abundance of cooperative breeding in birds and mammals, and diversity of life histories and ecological covariates observed in both of these groups, they have served as model groups for studying the evolution of reproductive cooperation. In both groups, large-scale comparative analyses of cooperative breeding have been published recently, taking advantage of complete and accurate phylogenetic data available for birds and mammals (Jetz and Rubenstein 2011; Lukas and Clutton-Brock 2012; Feeney et al. 2013). In all of these studies, as well as preceding work (Arnold and Owens 1998; Cockburn 1998, 2003), social systems were described in a binary fashion: species were either classified as cooperative breeders, where individuals help raising offspring that are not their own, or as noncooperative, where only parents are involved in raising offspring. The presence of helpers is a straightforward criterion, easily observable in the field, and provides an unequivocal definition of cooperative breeding and could be further revised to account for kin-based and nonkin cooperation (Riehl 2013). However, this binary categorization fails to account for an important feature of animal social systems—namely the formation of kin groups in the absence of cooperative breeding.

Kin groups usually arise when offspring delay their dispersal beyond independency and remain with their parents and siblings for a given period of time (Russell 2000). In some cases, this period

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(termed "family time" henceforth) is short, often short enough that such a strategy can be undistinguishable from dispersing right after reaching independence. However, in other cases, persistent family groups are formed, which usually is associated with various forms of nonreproductive kin cooperation (Dickinson and McGowan 2005; Griesser et al. 2006; Covas and Griesser 2007). A number of studies have pointed out that family living is an essential first step for the formation of cooperative breeding, as in almost all cooperatively breeding species offspring have first to delay dispersal and remain with their parents before they can become a helper at their parents' nest (Emlen 1994; Ekman et al. 2001, 2004). Thus, family living is likely to represent an intermediate strategy, fitting somewhere in the continuum of social systems between pair breeders and cooperative breeders. As such one might expect fundamental life-history differences between family living, non–family living, and cooperative breeding species and, consequently, merging non–family living and family living species might be partly responsible for equivocal and inconsistent results of comparative studies obtained so far (Covas and Griesser 2007; Griesser and Barnaby 2010). Yet, how should family living species be distinguished objectively from non–family living species?

Family time could provide a biological benchmark for this distinction. However, it would be too simplistic to classify as non–family living species only those where offspring disperse from parents, or parents abandon their offspring after reaching nutritional independence, as in many seabirds. Family times exhibit great variation and span from direct dispersal at independence to several years (Russell 2000). Species with short family time most likely are ecologically and evolutionarily more similar to species with zero family time. Thus, a threshold value of family time is needed in order to classify family living species. In such a way, a continuous measure directly describing the degree of parent–offspring association could be transformed into a categorical descriptor, supplementing the existing "cooperative breeding" category. The difficulty is finding an objective classification of this continuous quantity (i.e., family time) allowing to extract such threshold.

Here, we address the problem of defining family living by using a large data set of family time of nearly 750 bird species. We expect that evolution of delayed dispersal and family living would be associated with major changes in life-history traits, and thus, we predict that the footprint of these evolutionary processes should be visible in differences between family living and non–family living species. This evolutionary history would be reflected in a number of key eco-evolutionary traits associated with reproduction. Such traits could be used as benchmarks of life-history changes that arose due to breeding either in pairs or in larger family groups. However, such benchmark trait can only be used to measure differences between 2 groups. Locating the positions of the splitting point separating the groups requires a focal continuous variable that should be a straightforward extension of the desired nominal classification. An obvious choice in our case is the family time—as the trait directly measuring the degree of postindependence parent–offspring association. A more difficult task is finding a suitable benchmark variable, the values of which could guide us on the scale of focal variable.

To this end, we have used the body size–scaled initial reproductive investment (Sibly et al. 2012) as the benchmark variable of choice. We have used a simple numerical framework to define an objective threshold value of family time that best separates family and non–family living species. Breeding

investment is closely related to individual fitness and integrates various ecological and physiological factors that together shape the life history of a species (Martin 1987; Martin et al. 2006; Sibly et al. 2012). It is regarded as an accurate proxy of species reproductive strategy, placing it on the important slow–fast life-history axis. Moreover, it is available for substantially more taxa than other life-history parameters and as such represents the most widespread fitness-related measure currently available. We not only demonstrate how family time can be tied up with reproductive investment to yield the desired classification of family/non–family living species but also discuss how our novel classification relates to the expected differences between non–family and family living species in terms of their life history and ecology.

MATERIALS AND METHODS

The key temporal variable used in our study was family time, defined as the period of time the offspring delayed dispersal and stayed with their parents after reaching nutritional independence. We used unpublished data from a review paper (Russell 2000) and the major handbooks of birds (Maclean and Robert 1985; Cramp et al. 1994; Poole 2005; Higgins et al. 2007; Del Hoyo et al. 2011) to collect data on the family time together with detailed information on the remaining temporal characteristics of bird breeding (incubation period, nestling time, time to independence after leaving nest). The data on the reproductive investment (annual sum of clutch sizes per breeding pair in each species scaled by the female body mass, see below) were retrieved from a recent publication (Sibly et al. 2012) while we also gathered additional values on reproductive investment from the literature (see above). In total, we had data on family time, reproductive investment, and egg mass for 712 species, covering all major clades defined by the low-level phylogenetic backbone derived by Hackett et al. (2008; see also Jetz et al. 2012 for more details). Deliberately we have removed cooperatively breeding species from all analyses—their status and classification do not require any additional clarification: a binary criterion exists (i.e., presence or absence of predominant reproductive cooperation) that unambiguously defines them as cooperating or otherwise.

We used a body weight–scaled key parameter of reproductive investment (productivity index; Sibly et al. 2012) calculated as:

$$\pi_{\mathrm{m}} = \log\left(\frac{m_{\mathrm{e}} n_{\mathrm{e}} n_{\mathrm{c}}}{m_{\mathrm{f}}}\right),$$

where m_{e} is the egg mass, n_{e} the number of eggs per clutch, n_{c} the number of clutches per year, and m_{f} is the average female body weight. We adapted the productivity index proposed by Sibly et al. (2012) and used female body mass instead of male–female averaged mass, as the body weight of females—that is, the sex that physically produces the eggs—appears more appropriate as a reference for measuring reproductive investment. We repeatedly generated groups of family and non–family living species based on the family-time threshold varying between 2 and 150 days. Thus, we explicitly assumed that birds with family time < 2 days are classified as non–family living and species with family time > 150 days are classified as family living. We decided to stop at a family time of 150 days and classify all species with longer family times as family living for a number of reasons: 1) we do consider

species with family time >150 days as being certainly above the threshold and thus surely family living species and 2) beyond the 150 days threshold, the sample size in the 2 groups becomes very unbalanced as we successively classify more species as non–family living and less as family living (Supplementary Figure S1, for family time > 150 days, there are less than 25 species in family living group and more than 650 species in the non–family living group), which is likely to make the conclusion much less robust. For each of the 149 iterations, a mean productivity index (π_m) value was calculated for non–family and family living species. We then looked for the family-time threshold value that generates the maximum absolute difference in mean π_m between the 2 social systems.

To explore further how our categorization of social systems coincided with ecological conditions that might influence its evolution, we investigated the distribution of inferred social systems in relation to yearly seasonal changes and the mean growing season of the species distribution. The mean growing season describes overall plant vegetation timing in a given location (Michaletz et al. 2014) and strongly correlates with actual geographic location expressed as the absolute latitude of the centroid of species geographic distribution (Supplementary Figure S6). All models were analyzed using a generalized linear mixed model with a binomial distribution (a 2-state response variable: family living vs. non–family living; logit link function) in MCMCglmm (Hadfield 2010). The model included the phylogenetic effect to account for non-independence of species due to shared phylogenetic history. All runs were performed with 1 000 000 iterations, 250 000 burn-in period, and samples taken from the posterior distribution of estimated fixed and random effect parameters every 1000 iterations (resulting in effective sample size of approx. 1000). Phylogenetic signal was calculated as the intraclass correlation coefficient at the level of the phylogenetic random effect according to Hadfield (2014).

In order to ensure that the results are valid and do not result from statistical artifacts, we have performed a number of validations based on simulation and bootstrapping. The details on each of the validation methods can be found in the Supplementary Materials and methods.

It is difficult to construct analytically sampling error measures for the estimated parameter. First, randomizing/resampling the data tends to generate functional relationships of several kinds between the difference in π_m and family-time threshold (depending on the iteration we were able to fit, e.g., logistic, polynomial, exponential to the resulting pattern). Thus, automatically extracting the threshold value—which could be used to construct approximate sampling distribution—is difficult. To provide a surrogate of sampling distribution, we have used the following strategy: 1) we generated 1000 subsets of data by bootstrapping (resampling with replacement) rows of original data set; 2) for each subset performed threshold search; 3) fitted a segmented piecewise regression to the resulting pattern (package segmented; Muggeo 2003) to extract the breaking point of the pattern, indicating the maximum observed value (most patterns either plateau or reach maximum at this value; in both cases, the breaking point accurately identifies the threshold—in case of the original pattern—Figure 1—this breaking point is equivalent to edge of the plateau, i.e., family time = 50 days); 4) constructed a sampling distribution of 1000 estimated breaking points, which will necessarily be centered around the original estimated threshold.
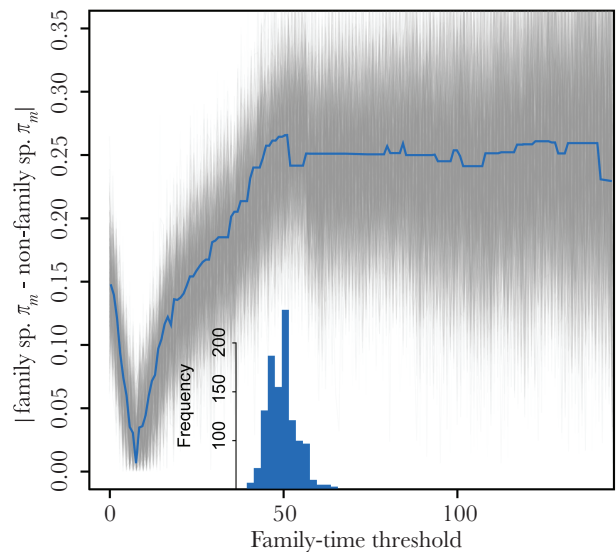
Figure 1
Difference in annual mass–scaled productivity index (π_m) between family living and non–family living species in relation to the family-time threshold used to differentiate the 2 groups. Blue line represents original pattern, and gray lines depict patterns obtained for bootstrapping samples drawn from the data. The approximate sampling distribution of the threshold value of family time is shown as a histogram on the horizontal axis.

RESULTS

The shifting-threshold approach indicated a maximal difference in initial breeding investment between resulting non–family and family living species for a cutoff value of 50 days (Figure 1). Using this 50-day threshold resulted in 529 species classified as non–family living and 104 species being classified as family living. The remaining 79 species are cooperative breeders and were not included in our analyses as the definition of cooperative breeding is unambiguous. Bootstrapping of family-time values reveals noise around the original pattern, mostly generated by resampling random species from a continuum of family times—vast majority of samples, however, successfully replicate the 50-day threshold (see histogram, Figure 1).

Four different validation methods all supported the 50 days threshold (see Supplementary Materials and methods). In particular, phylogenetically corrected values recapitulated the pattern observed in raw means (Supplementary Figure S1). Randomized samples (see Supplementary Materials and methods: validation 2 and 3) did not exhibit the pattern observed in the original data (Supplementary Figures S2 and S3). Moreover, the pattern also was confirmed when equal sizes of social system groups were used by resampling them for each threshold value with replacement (see Supplementary Materials and methods: validation 4 and Supplementary Figure S5). It is important to note that the choice of the start of the plateau in Figure 1 is only one possibility. One might argue that instead of using the first observed plateau observation, it might be more suitable to shift the threshold further along the plateau toward greater values of family time or place it at some other unambiguous points along the estimated line (e.g., the inflection point located between 10 and 50 days of family time, equivalent to roughly a half of maximum observed difference between family and non–family breeding species). However, any other placement of the threshold would result in a less parsimonious conclusion (putting the threshold further on the plateau would result in

including as non–family breeding individuals those that do not contribute to predicted differences in reproductive allocation and at the same time have abnormally long family times) or in classification that is not stable in terms of life-history parameters (putting the cutoff at the inflection point would yield where differences between the 2 resulting groups would be very sensitive to even small changes of the chosen classification threshold).

Independently of family-time considerations, an interesting effect concerning total breeding period became apparent in our data. Combined data on incubation and nestling time with the time to independence and family time indicated that in most non–family living species, offspring dispersed the latest 150 days after the onset of breeding (Figure 2). In contrast, in the majority of family living species, dispersal of offspring occurred later than 150 days after the onset of breeding (Figure 2). In non–family living species, offspring dispersal occurred later than 150 days in only 14 cases and the majority of those species have the centroid of their geographical distribution in low latitude regions (Figure 3). Similarly, the majority of family living species where offspring disperse before 150 days from the start of breeding ($n = 24$ species) occurred mostly in temperate regions or resided in both temperate and tropical climate (Figure 3). This was further confirmed by an interaction between total breeding period (total time from egg laying to offspring dispersal) and the mean growing season of the species distribution in a mixed model looking at the probability of observing a particular breeding system (Supplementary Table S1). The interaction indicates that the probability of being a family living species increases with total time spent with parents (sum of all predispersal periods) in regions of long mean growing season (i.e., low latitudes) but decreases with increasing total time spent with parents in regions where the mean growing season is shorter (i.e., latitude increases) (Supplementary Table S1). The generalized mixed model confirmed that the social system (family living vs. nonfamily breeding) is highly phylogenetically structured
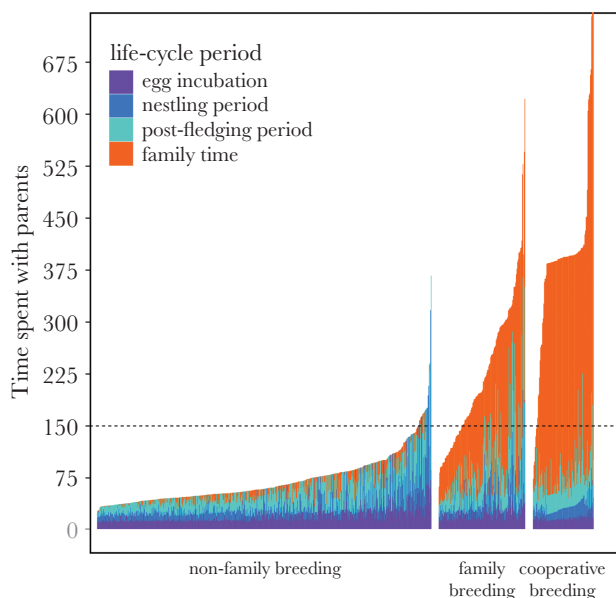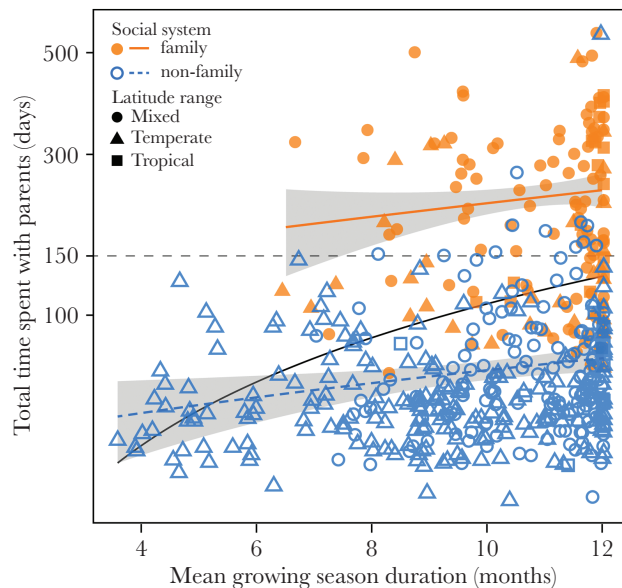
Figure 3
Association between the total time offspring spent with their parents (from onset of incubation to dispersal, in days), the mean growin season of species distribution, and the range of latitudes occupied by each species. The line lacking confidence band depicts overall relationship in all species, the two lines with confidence bands show relationships in the 2 social breeding systems. The 150 day cutoff (see text) is indicated with a dashed horizontal line.
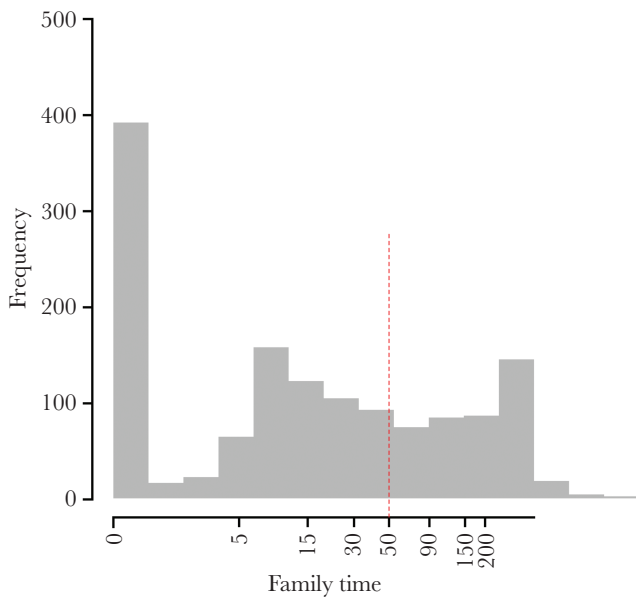
(phylogenetic heritability and its 95% highest posterior density interval—on the link function scale: 0.67 (0.54; 0.87); on the scale of data: 0.94 (0.87; 1.06)).

The estimated threshold that we use to categorize social systems in birds coincides with a natural hiatus in the distribution of family times (Figure 4). Excluding family times equal to zero, the distribution is bimodal with a ridge around the value of 50 days (Figure 4). Interestingly, when including zero family times, the distribution is trimodal as most species tend to disperse directly after achieving independence. This first gap separates species having zero and nonzero family time and thus, for reasons explained in the Introduction and the Materials and Methods, cannot be used as a suitable threshold to define families.

DISCUSSION

Our results confirm that social breeding systems are more heterogeneous than previously appreciated (but see Russell 2000). Using birds as a model system and a central life-history trait, the annual reproductive investment, we demonstrate that noncooperatively breeding species are heterogeneous in terms of the postindependence offspring dispersal and can be further divided into 2 distinct categories. One of the most easily observable features of social breeding—namely, the formation of persistent groups composed of kin individuals delaying their dispersal—occurs also in species lacking any traces of reproductive cooperation. However, contrary to reproductive cooperation, classifying family living species is more ambiguous as it cannot be assessed based on a bicategorical descriptive behavior. The fact that offspring in some species remain some time beyond independency with their parents may just reflect variation in dispersal timing as found in many species, or behavioral inertia in moving from one phase of

Figure 2
The distribution of total times that offspring spend with their parents, subdivided into respective periods of the lifecycle and in relation to 3 categories of social breeding defined using our approach. The 150-day limit is indicated with a dashed line (see Discussion for more details).

Figure 4
Distribution of family times in 1103 bird species. Dashed line indicates the 50-day family-time threshold that was chosen to separate family living and non–family living species.

life cycle to the other, particularly if short delays in dispersal are costly to neither parents nor offspring. Our approach provides an objective way of finding the critical family-time value that results in the biggest difference between the 2 social systems. Moreover, the result coincides with naturally observed discontinuity in the distribution of family times in our larger set (i.e., including species for which we did not have the productivity index and that could not be included in the main analysis). Although similar considerations relating delayed dispersal and breeding ecology have been made in evolutionary biology (e.g., Russell et al. 2004), our approach is unique in providing an actual definition that is based on measurable properties of bird reproductive biology. Importantly, our analyses have proved to be robust to all statistical artifacts that might generate similar results—all validation procedures confirmed the presence of the observed pattern and supported its uniqueness (in both randomization analyses that break association between productivity and family time, the pattern disappeared).

Annual productivity (π_m) is a central and fundamental life-history variable (Sibly et al. 2012), reflecting adaptations of bird life histories to varying ecological conditions (Lack 1968; Griebeler et al. 2010; Sibly et al. 2012). Thus, it is also affecting the link between social systems and reproductive strategies (Emlen 1994; Arnold and Owens 1998; Cockburn 1998; Covas and Griesser 2007). Splitting non–family living and family living species according to a threshold value of family time equal to 50 days maximizes the difference in annual investment observed in these 2 groups. On average, non–family living species have a higher annual productivity compared with family living ones, confirming studies indicating that delayed dispersal is more frequent in species with low adult mortalities and low reproductive output (Arnold and Owens 1998; Ekman et al. 2001; Russell et al. 2004). The difference is substantial—non–family living species produce on average 1.5 times more eggs per year per unit of body mass than family living taxa. It is possible that the

strategy of forming family groups buffers out costs of rearing offspring and results in being able to maintain similar overall success with a lower annual productivity. Alternatively, delayed dispersal, while being beneficial to the offspring, may be costly for parents—forcing them to decrease their reproductive output considerably and favoring offspring quality over quantity. Although our study does not point to one particular alternative, we hope it will stimulate further research toward understanding costs and benefits of family living.

Why is the 50-day threshold a biologically meaningful cutoff to define family living? In nontropical climatic zones, the period of year comprising the most favorable conditions for breeding spans over approx. 150 days (rounded to full months; mean 155.72 ± 10.49 days [www.weatherbase.com, accessed 5 December 2014]; favorable conditions defined as months with average temperature greater or equal to 11 °C, the temperature associated with an average large-scale vegetation onset in temperate locations and the start of the optimal photosynthetic activity; Morison and Morecroft 2006) and starts roughly in April/May in the northern hemisphere (respectively in September/October in the southern hemisphere), concluding with a decrease in food abundance and an onset of less favorable conditions in September in the northern hemisphere (respectively March in the southern hemisphere) (Morison and Morecroft 2006). For most non–family living species, the total breeding period is shorter than 150 days (Figure 2) and hence does not progress beyond this boundary of worsening conditions. The total breeding period of most family living birds, however, exceeds 150 days (Figures 2 and 3). The outcome of our analysis reveals an ecological footprint of the evolution of family living with respect to seasonally occurring unfavorable conditions (Russell 2000). Delaying dispersal beyond autumn may only be possible in species where offspring can benefit from prolonged association with their parents, increasing their survival (Ekman et al. 2001; Covas and Griesser 2007). Our approach indicates that these benefits may outweigh costs of family living only if it is associated with long-enough association of individuals forming a family group.

Relating family and non–family living to the assumed 150 days period of unfavorable conditions (Figure 3) reveals yet another interesting biogeographical pattern: all pair-breeding species that live in high latitudes lie below this line, whereas all the remaining (pair and family breeding) species laying above this line live exclusively in mid- and low latitudes. Thus, prolonged parental care and delaying dispersal seem to be ecologically constrained in high latitudes but provide clear advantage in lower latitudes, shifting the distribution of kin-group forming species toward lower latitudes (Russell 2000). The nature of this constraint requires further research: it is possible that solely climatic constraints prevent birds from delaying dispersal into harsher and less viable conditions; however, other factors contributing to delayed dispersal (e.g., access to high-quality territories inherited from parents) also may be latitude constrained.

Interestingly, in both groups, there are species that do not match this 150-day criterion. Apart from random noise in the data (i.e., inaccurate data on family time—or timing of any other part of the reproductive cycle), such cases may be explained by accounting for geographical distribution of such species. Most non–family living species crossing the 150 days' timeline come from low absolute latitude regions (i.e., tropical/subtropical) or are widespread species with mixed climatic preferences. Similarly, family living species with total breeding period below 150 days tend to be temperate

climate ones. Thus, mismatches occur mostly in cases where the 150-day threshold may not be accurate and limiting, supporting our result.

The consequences of this new classification for our understanding of the evolution of social behavior in birds still remain to be explored. Our preliminary results not presented here indicate that discrepancies between the traditional and new classification of social breeding systems are substantial. For example, our classification significantly alters observed associations between social system and environmental unpredictability in terms of environmental dependency of cooperative breeding, extending and greatly clarifying earlier analyses (e.g., Jetz and Rubenstein 2011). Our analyses indicate that merging together nonfamily and family breeders erroneously associates 2 very different strategies, and in terms of environmental sensitivity, family breeders are more similar to cooperative breeders (Griesser et al. 2014). Moreover, family living taxa exhibit markedly higher levels of sexual body size dimorphism compared with non–family living and cooperatively breeding species, which emphasizes the great evolutionary uniqueness of family breeding in terms of sexual selection pressure and how it is related to overall life-history patterns in birds (Drobniak et al. 2014).

To conclude, our life-history-based approach shows that cooperative breeding and non–family living are not the only alternatives on the scale of social modes in birds. Family living in the absence of cooperative breeding represents an intermediate state, which hitherto has not received sufficient attention. More importantly, family living may represent a transition stage in the evolution of cooperative breeding as almost all cooperative breeding birds live in family groups (Riehl 2013). Using family living as an intermediate social system, one can provide a more parsimonious, multistage description of how cooperative breeding might have evolved in birds (Emlen 1994; Ekman et al. 2004; Covas and Griesser 2007). Appreciating this social system will open new research perspectives and solve existing inconsistencies in our understanding of the evolution of cooperation.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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REFERENCES

Arnold KE, Owens IPF. 1998. Cooperative breeding in birds: a comparative test of the life history hypothesis. Proc R Soc B. 265:739–745.
Cockburn A. 1998. Evolution of helping behavior in cooperatively breeding birds. Annu Rev Ecol Syst. 29:141–177.
Cockburn A. 2003. Cooperative breeding in oscine passerines: does sociality inhibit speciation? Proc R Soc B. 270:2207–2214.

Covas R, Griesser M. 2007. Life history and the evolution of family living in birds. Proc R Soc B. 274:1349–1357.
Cramp S, Simmons KE, Perrins CM, Brooks DJ. 1994. Handbook of the birds of Europe, the Middle East and North Africa. Oxford: Oxford University Press.
Darwin C. 1859. On the origin of species. London: John Murray.
Del Hoyo J, Elliot A, Sargatal J, Christie DA. 2011. Handbook of the birds of the world. Barcelona (Spain): Lynx Editions.
Dickinson JL, McGowan A. 2005. Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. Proc R Soc B Biol Sci. 272:2423–2428.
Drobniak SM, Dunn P, Griesser M. 2014. Sex in the family. Abstracts of the 15th International Behavioral Ecology Congress; 2014 August 11–15; New York (NY).
Ekman J, Baglione V, Eggers S, Griesser M. 2001. Delayed dispersal: living under the reign of nepotistic parents. Auk. 118:1–10.
Ekman J, Dickinson JL, Hatchwell BJ, Griesser M. 2004. Delayed dispersal. In: Koenig WD, Dickinson JL, editors. Ecology and evolution of cooperative breeding in birds. Cambridge (UK): Cambridge University Press.
Emlen ST. 1994. Benefits, constraints and the evolution of the family. Trends Ecol Evol. 9:282–285.
Feeney WE, Medina I, Somveille M, Heinsohn R, Hall ML, Mulder RA, Stein JA, Kilner RM, Langmore NE. 2013. Brood parasitism and the evolution of cooperative breeding in birds. Science. 342:1506–1508.
Griebeler EM, Caprano T, Bohning-Gaese K. 2010. Evolution of avian clutch size along latitudinal gradients: do seasonality, nest predation or breeding season length matter? J Evol Biol. 23:888–901.
Griesser M, Barnaby J. 2010. The role of nepotism and competition for the evolution of avian families. New York: Nova Publisher.
Griesser M, Drobniak SM, Nakagawa S, Botero C. 2014. The rise and fall of cooperative and family living in birds. Abstracts of the 1st Modern Phylogenetic Comparative Methods Conference; 2014 November 10–14; Sevilla, Spain.
Griesser M, Nystrand M, Ekman J. 2006. Reduced mortality selects for family cohesion in a social species. Proc R Soc B. 273:1881–1886.
Hackett SJ, Kimball RT, Reddy S, Bowie RC, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han KL, Harshman J, et al. 2008. A phylogenetic study of birds reveals their evolutionary history. Science. 320:1763–1768.
Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. J Stat Softw. 33:1–22.
Hadfield JD. 2014. MCMCglmm course notes [cited 2015 March 11]. Available from: http://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf.
Hamilton WD. 1964. Genetical evolution of social behaviour I. J Theor Biol. 7:1–16.
Hatchwell BJ. 2009. The evolution of cooperative breeding in birds: kinship, dispersal and life history. Phil Trans R Soc B Biol Sci. 364:3217–3227.
Higgins PJ, Marchant S, Peter JM, Cowling S, Davies J. 2007. Handbook of Australian, New Zealand & Antarctic birds. Oxford (UK): Oxford University Press.
Jetz W, Rubenstein DR. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Curr Biol. 21:72–78.
Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. Nature. 491:444–448.
Lack D. 1968. Ecological adaptations for breeding in birds. London: Methuen.
Lukas D, Clutton-Brock T. 2012. Life histories and the evolution of cooperative breeding in mammals. Proc R Soc B Biol Sci. 279:4065–4070.
Maclean GL, Robert A. 1985. Robert's birds of southern Africa. Cape Town (South Africa): Trustees of the John Voelcker Bird Book Fund.
Martin TE. 1987. Food as a limit on breeding birds—a life-history perspective. Annu Rev Ecol Syst. 18:453–487.
Martin TE, Bassar RD, Bassar SK, Fontaine JJ, Lloyd P, Mathewson HA, Niklison AM, Chalfoun A. 2006. Life-history and ecological correlates of geographic variation in egg and clutch mass among passerine species. Evolution. 60:390–398.

Michaletz ST, Cheng D, Kerkhoff AJ, Enquist BJ. 2014. Convergence of terrestrial plant production across global climate gradients. Nature. 512:39–43.

Morison JIL, Morecroft MD. 2006. Plant growth and climate change. Oxford: Blackwell Publishing Ltd.

Muggeo VMR. 2003. Estimating regression models with unknown breakpoints. Stat Med. 22:3055–3071.

Poole A. 2005. The birds of North America online [cited 3 March 2015]. Ithaca (NY): Cornell Laboratory of Ornithology. Available from: http://bna.birds.cornell.edu/bna.

Riehl C. 2013. Evolutionary routes to non-kin cooperative breeding in birds. Proc R Soc B Biol Sci. 280:20132245.

Russell EM. 2000. Avian life histories: is extended parental care the southern secret? Emu. 100:377–399.

Russell EM, Yom-Tov Y, Geffen E. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behav Ecol. 15:831–838.

Sibly RM, Witt CC, Wright NA, Venditti C, Jetz W, Brown JH. 2012. Energetics, lifestyle, and reproduction in birds. Proc Natl Acad Sci USA. 109:10937–10941.