Cooperative breeding is not very common in birds but intriguingly over-represented in some avian families particularly in the Australasian and Afro-tropical realms [2–4]. Over-representation suggests that predisposing traits, similar ecological constraints or both act to facilitate the occurrence of cooperative breeding in these families. Finding the ultimate factors underlying cooperative breeding remains a major challenge [5].

Discussion of predisposing traits in birds has centred on high adult annual survival, an indication of a slow pace of life. By increasing the pool of available breeders in a limited environment, high annual survival would increase competition for breeding opportunities, facilitating the delayed dispersal of offspring and helping [6,7]. Cooperative breeders should also produce smaller clutches because of the typical trade-off between fecundity and adult survival [8]. In addition, smaller clutches may occur more frequently in cooperative breeders in response to selection against the production of additional offspring that would fare poorly in the more competitive habitat [9].

While early comparative analyses in birds failed to find support for an association between adult annual survival and cooperative breeding [10–12], a more recent and influential comparative analysis in birds suggested that high adult annual survival and small clutch sizes were more common in cooperative breeders and that families of birds with more cooperative breeders showed higher adult survival but not smaller clutches [2]. This life-history hypothesis has gained support and has formed the basis of several theoretical analyses of cooperative breeding in animals [13–15].

Some scepticism has been raised concerning the life-history hypothesis because life-history theory predicts a strong correlation between adult annual survival and clutch size but only annual survival and not clutch size has been found to be associated with cooperative breeding in birds at the family
level [16]. A recent review also suggested that the distinction between cooperative and non-cooperative lineages, which would produce the expected difference in lifespan and survival, may not be as strong as predicted [17]. I also note that while many cooperative breeders were included in the Arnold and Owens study, the actual sample size to evaluate the association with adult annual survival was quite small (n = 27), which raises the possibility that the results may not be applicable in general. Adult annual survival must be associated with body mass, in the sense that larger species typically live longer [18], but body mass was not included as a cofactor in their analysis. This is also an issue for clutch size, which tends to be negatively associated with body mass in birds [19]. Taking into account potential confounding factors, a recent analysis failed to document an association between maximum longevity and cooperative breeding in North American birds [20], but did not address the relationship with clutch size. In addition, North America is not a hotspot of cooperative breeding in birds, and it is not clear whether the results there apply to realms where cooperative breeding is more prevalent.

Here, I re-examine the life-history hypothesis in a large sample of species taken from all parts of the world. I used two proxies of a slow pace of life, namely, maximum longevity and adult annual survival. Maximum longevity can only be obtained from ring recoveries or resightings of known-aged birds. As such, estimates of maximum longevity will typically increase with the number of recoveries [20,21], which should be controlled to avoid potential biases. Nevertheless, the use of maximum longevity to estimate lifespan is controversial, and other sources of bias have been discussed [22], which makes such estimates not quite as reliable as adult annual survival rate. Unfortunately, estimates of annual survival rate are less common in the literature reducing the power to detect differences. Correlates of longevity have been uncovered recently and must be taken into account when comparing cooperative and non-cooperative breeders. A thorough review in birds has shown that maximum longevity is associated with diet and body mass [23]. Cooperative and non-cooperative breeders also show differences in body mass and diet [4], no. 9792). I thus tested the life-history hypothesis by controlling for sampling effort, body mass and diet.

2. Material and methods

(a) Selection of species and ecological variables

I used the list of avian cooperative species compiled by Jetz & Rubenstein [4]. This list greatly overlaps the earlier one used by Cockburn [1]. The list of cooperative species continually evolves as additional information becomes available, especially for the lesser known tropical species. Therefore, I also sampled the recent literature to uncover new published cases of cooperative breeding (see the electronic supplementary material for a list of species).

I included in the dataset all cooperative species where information about maximum longevity or adult annual survival rate was known. Maximum longevity in a species corresponds to the age of the oldest individual recaptured or resighted, or whose ring has been recovered in the field. Maximum longevity was obtained from the most recent ringing reports available from North America (Bird Banding Laboratory, Patuxent Wildlife Research Center), Europe (Euring [24]), Australia (Australia Bird and Bat Banding Scheme) and South Africa (SAFRING, Avian Demography Unit, University of Cape Town). These datasets were accessed in the autumn of 2013. In addition, I consulted the literature to obtain longevity estimates from research papers and also contacted researchers to get similar information from their own ringing efforts with individual species. The number of recoveries, which forms the basis to estimate longevity, was available from these lists or from the researchers. Recoveries include recaptures or resightings of previously ringed individuals or ring recoveries.

Adult annual survival rate was available for a more restricted number of species. These estimates are based on capture/recapture data collected over a number of years. When estimates were provided separately for males and females, I selected data for males to go along with the more frequent estimates of male body mass available in the literature (see below). For North American species, I relied on the Monitoring Avian Productivity and Survivorship programme of the Institute for Bird Population (Point Reyes, California). For other areas, I relied on estimates available from the general avian literature.

I matched each selected cooperative species with the most closely related non-cooperative sister species with sufficient information about breeding system and the various ecological variables mentioned earlier. I used recent molecular phylogenetic trees (see the electronic supplementary material for references) to perform the matching. Such close matching will reduce variation between species in a pair in a number of ecological and physiological traits, which may affect longevity. I ensured that an imaginary line linking the two species of a pair on the phylogenetic tree did not overlap with any lines from other pairs so as to treat a pair as the independent unit of analysis [25]. In a few cases where the phylogenetic affinities of a cooperative breeder were not fully resolved, I used a sister species from the same genus.

From published sources, I obtained the following information for each species: the geographical realm (Nearctic, Neo-tropical, Palearctic, Afro-tropical, Indo-Malayan, Australasian or Oceanic), for each species: the geographical realm (Nearctic, Neo-tropical, Palearctic, Afro-tropical, Indo-Malayan, Australasian or Oceanic), for each species: the geographical realm (Nearctic, Neo-tropical, Palearctic, Afro-tropical, Indo-Malayan, Australasian or Oceanic), and also classified the frequency of cooperative breeding as unusual or not (less than 10% of monitored nests with more than two parents) based on the information provided by Cockburn [1].

(b) Statistical analysis

All quantitative variables were log10 transformed prior to the analysis except for adult annual survival rates, which were converted using the arcsine-square-root transformation. For maximum longevity, I used a mixed linear model with pair identification (ID) as a random factor, breeding type (cooperative or not) as a fixed factor and body mass and number of recoveries as cofactors. I also considered a squared term for number of recoveries to model a possible nonlinear relationship between longevity and reproductive variables (tolerance 0.8). I repeated the above analysis using various subsamples of the original dataset. These analyses were carried out to evaluate the robustness of the findings based on the full dataset. The first subsample excluded unusual cooperative breeding species. The second subsample excluded cooperative species without group territoriality. The third subsample only included pairs where the sample size for the number of recoveries was larger than 50. The final subsample only included pairs where annual survival rate was known.

For estimates of adult annual survival rate and clutch size, I used a mixed linear model with pair ID as a random factor, breeding type (cooperative or not) as a fixed factor and body mass as
Results

The dataset consisted of 124 pairs of closely related species including one cooperative breeder and one non-cooperative breeder (electronic supplementary material). The cooperative breeders came from all realms (Australasian: 37%; Afro-tropical: 19%; Nearctic: 16%; Neotropical: 14%; Palearctic: 10%; Indo-Malayan: 3% and Oceanic: 1%). Cooperative breeders belonged to 56 different families. The number of pairs with full data for maximum longevity was 81 and 37 for adult annual survival.

Maximum longevity increased linearly with body mass ($b \pm$ (s.e.m.): $F_{1.76} = 16.0, p = 0.0001$) and the number of recoveries ($b \pm$ (s.e.m.): $F_{1.76} = 67.7, p < 0.0001$). Controlling for these two cofactors, the expected maximum longevity did not vary according to breeding type ($F_{1.76} = 0.67, p = 0.42$; figure 1a).

Subsample analyses of the data also failed to uncover a statistically significant effect of breeding type on maximum longevity. This was the case in the subsample of the data excluding unusual cooperative breeders ($F_{1.69} = 0.63, p = 0.43$), in the one excluding cooperative breeders without group territoriality ($F_{1.35} = 0.36, p = 0.56$), in the one excluding species with fewer than 50 recoveries ($F_{1.25} = 0.57, p = 0.46$) and, finally, in the one excluding species with no information about adult annual survival rate ($F_{1.31} = 0.09, p = 0.77$).

Adult annual survival rate was higher by about 10% in the cooperative than in the non-cooperative breeders ($F_{1.38} = 9.9, p = 0.003$; figure 1b), controlling for the positive effect of body mass ($F_{1.35} = 34.0, p < 0.0001$). There was no statistically significant correlation between the contrasts in adult annual survival rate and maximum longevity ($r = -0.051, p = 0.77, n = 34$). Mean clutch size did not differ statistically between the two types of species ($F_{1.90} = 0.04, p = 0.85$; figure 1c), controlling for the negative effect of body mass ($F_{1.90} = 10.4, p = 0.002$).

There was no difference between the two types of species in the mean number of recoveries (back-transformed means (95% confidence interval); CI): cooperative breeders: 89.6(52.8–152.1) and non-cooperative breeders: 61.3(32.4–115.9); $F_{1.80} = 1.6, p = 0.21$ and mean male body mass ($F_{1.115} = 0.17, p = 0.68$; figure 1d). In the 117 pairs where diet was known for each species, the two types of species showed a similar type of diet in all but 20 pairs (17.1%), with no directional transitions between diet types in the discordant pairs ($S = 1.51, p = 0.68$).

Discussion

I used a global dataset including closely related species of birds that differ with respect to the occurrence of cooperative breeding to determine whether cooperative breeders live longer and have smaller clutches, as expected from the life-history hypothesis. Matching of closely related pairs of species reduced other differences in ecological factors that may contribute to differences in lifespan and clutch size.
Indeed, the two types of species did not differ in male body mass or in diet. The number of recoveries, which forms the basis to estimate maximum longevity, also did not vary with breeding type. Controlling for these potential correlates, I could not find any statistically significant effect of breeding type on maximum longevity. In a smaller dataset, adult annual survival rate was higher in the cooperative breeders, controlling for body mass. There was no association between cooperative breeding and clutch size.

The discrepancy in the results from the two proxies of a slow pace of life pinpoints weaknesses in the use of maximum longevity to estimate lifespan. This difference is not simply the result of sampling different species because maximum longevity was not associated with cooperative breeding in the dataset where adult annual survival rate was higher in the cooperative breeders. The lack of association also persisted in various subsamples of the data where the expected effect on maximum longevity may be stronger. Estimates of maximum longevity are by definition based on the extreme of the survival curve in a population. Obviously, more intensive sampling will generally increase the odds of capturing the older individuals. This sample size effect was controlled here by including the number of recoveries as a cofactor in the model. Other sources of bias have been discussed, and estimates of maximum longevity are typically considered biased [22]. The lack of association between estimates of maximum longevity and adult annual survival rate in my sample corroborates this conclusion.

I found mixed evidence for the life-history hypothesis. Adult annual survival was indeed higher in the cooperative breeders but clutch size was not smaller. Comparative analyses of North American birds [20] and mammals [26] failed to find a relationship between cooperative breeding and maximum longevity but, as discussed above, maximum longevity may be a poor proxy to evaluate the life-history hypothesis. The comparative analysis of Arnold & Owens [2] found higher adult survival and smaller clutch sizes at the species level but found a weaker association with clutch size at the family level. It is not clear how such patterns would hold controlling for body mass, as was done here.

While in the predicted direction, the association between adult annual survival and cooperative breeding was moderate. The moderate association between adult annual survival and cooperative breeding may not have been sufficient to bring clutch size down over evolutionary times. In fact, many ecological factors influence the size of a clutch in birds, including body mass, climate, diet and migration behaviour [19]. It is perhaps the case that the moderate effect of adult annual survival may have been swamped in the process. When more estimates of annual survival rate become available, the reduction in clutch size may be more apparent in clades where the increase in adult annual survival is stronger.

Information about maximum longevity or adult annual survival rate was available for less than 15% of the currently known cooperative breeders of birds, which raises the possibility of sampling biases. Information about lifespan requires long-term studies and extensive ringing programmes, which typically tip the balance in favour of species from North America, Europe and Australia, and to some extent southern Africa, leaving other geographical realms largely unexplored. As a case in point, Jetz & Rubenstein [4] found an association between cooperative breeding and factors such as body mass and diet in their worldwide study while no such association was documented here in a more restricted sample. Overall, the results of my analysis provide partial support for the life-history hypothesis but a stronger case awaits additional data on adult annual survival rate in birds.

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