

Direct benefits and evolutionary transitions to complex societies

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The selective forces that drive the evolution of cooperation have been intensely debated. Evolutionary transitions to cooperative breeding, a complex form of cooperation, have been hypothesized to be linked to low degrees of promiscuity, which increases intragroup relatedness and the indirect (that is, kin selected) benefits of helping. However, ecological factors also promote cooperative breeding, and may be more important than relatedness in some contexts. Identifying the key evolutionary drivers of cooperative breeding therefore requires an integrated assessment of these hypotheses. Here we show, using a phylogenetic framework that explicitly evaluates mating behaviours and ecological factors, that evolutionary transitions to cooperative breeding in cichlid fishes were not associated with social monogamy. Instead, group living, biparental care and diet type directly favoured the evolution of cooperative breeding. Our results suggest that cichlid fishes exhibit an alternative path to the evolution of complex societies compared to other previously studied vertebrates, and these transitions are driven primarily by direct fitness benefits.

Cooperative breeding, where individuals in social groups provide care for offspring that are not their own, is a complex form of sociality¹ that has arisen repeatedly across the animal kingdom. Cooperative breeders are of great interest for evolutionary biologists, as individuals that forgo their own reproduction appear to oppose Darwin's fundamental argument that selection acts on differential reproductive success². Kin selection³ emerges as the most prominent explanation for this apparently paradoxical behaviour, where non-breeding helping individuals can gain 'indirect' fitness benefits by increasing the reproductive success of relatives. Consequently, the evolution of cooperative breeding is hypothesized to be favoured when females exhibit relatively low levels of promiscuity^{1,4–6}, thereby generating high within-group relatedness among offspring. Indeed, lifetime monogamy, which generates social groups containing full siblings, is inferred to be the ancestral state that preceded the transition to complex sociality in eusocial insects^{5,6}. Among birds¹ and mammals⁴, evolutionary transitions to cooperative breeding have been linked with low degrees of promiscuity. Together, these results support the role of kin selection and indirect fitness benefits as key evolutionary drivers of complex cooperative societies.

However, many other studies have demonstrated a strong relationship between ecological and life-history factors and the evolution of cooperative breeding^{7–11}. In some cases, ecological factors can facilitate kin selection regardless of the level of female promiscuity^{8,12}, for example when constraints on dispersal and independent breeding create kin neighborhoods. However, ecological factors can also contribute to direct fitness benefits for helpful individuals¹³, for example by offering helpers protection from predators or providing reproductive opportunities. The strong link between ecological factors and cooperative breeding complicates our understanding of the

evolution of cooperative societies, because social monogamy is also favoured under particular ecological factors¹⁴ and therefore apparent relationships between monogamy and cooperative breeding could actually be driven by relationships between ecology and cooperative breeding^{15,16}. However, because previous attempts to understand the evolutionary origins of cooperative breeding have evaluated the importance of promiscuity/monogamy^{1,4–6} or ecological hypotheses^{7–9} independently, the relative importance of these alternative selective factors in promoting cooperation remains unclear¹⁴.

This lack of an integrated approach not only prevents an assessment of the relative importance of female promiscuity for the evolution of cooperation, but has also generated debate about how sexual selection operates in highly social species^{17,18}. Several studies have found that cooperative breeding species have reduced sexual dimorphism, relative to non-cooperative species^{17,19}. Although this pattern could be driven by high reproductive skew and strong intrasexual selection on both sexes in cooperative breeders¹⁷, it may also simply be an evolutionary artifact of cooperative breeding evolving from monogamous ancestors that exhibit low levels of sexual dimorphism¹⁸. Consequently, clarifying the role that monogamy plays in the evolution of cooperative breeding will have important implications for our understanding of both kin selection and sexual selection in highly social species.

Here, we evaluate the importance of multiple factors hypothesized to promote evolutionary transitions to cooperative breeding in lamprologine cichlid fishes. Lamprologines are endemic to Lake Tanganyika, the oldest of the African Great Lakes, and account for roughly 40% of cichlid biodiversity in this lake²⁰. This group contains non-cooperative and obligate cooperative breeding species, and are the only fishes in the world that exhibit true cooperative breeding (Fig. 1). Cooperative breeding cichlids form permanent

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social groups where dominant breeders and non-reproductive subordinate helpers engage in collective nest tending and territory defence²¹. The genetic structure of cooperative groups has been evaluated in a handful of cooperative cichlid species. In most species studied to date, helpers typically exhibit low levels of within-group relatedness (for example, *Neolamprologus pulcher*, *N. savoryi*, *Julidochromis ornatus*; see Methods), although in at least two cooperative species helpers are highly related to dominant breeders (*N. multifasciatus* and *N. obscurus*). Therefore, the best available evidence suggests that cooperatively breeding cichlid social groups are not typically family groups, but vary between groups made up of individuals that are distantly or unrelated, and occasionally groups that are close relatives. Thus, unlike other cooperatively breeding vertebrates where indirect benefits drive the evolution of cooperative breeding^{1,4}, in cichlids the low levels of within-group relatedness suggests that direct benefits may be more important in driving evolutionary transition to cooperative breeding. However, despite extensive study of cooperative behaviour in lamprologine species²¹, we currently have a poor understanding of factors related to the evolution of cooperative breeding across this clade of fishes.

Results and discussion

To determine the key evolutionary factors promoting cooperative breeding in lamprologine cichlids, we categorized each species' social system as either non-cooperative or cooperative breeding based on whether they had helpers, and compiled available data on key ecological and life-history traits that have been linked to cooperative breeding (Supplementary Table 1; data were available for 69 out of a total of approximately 80 species). To account for evolutionary history, we created a phylogeny using Bayesian likelihood methods applied to nuclear and mitochondrial DNA sequences. We then mapped social systems onto this phylogeny and performed ancestral state reconstructions of social system, revealing five independent evolutionary transitions to cooperative breeding and one loss of cooperative breeding among lamprologine cichlids (Fig. 1e).

We then used two complementary approaches to test whether transitions to cooperative breeding were more likely in species with monogamous ancestors. Prior to analyses, species were classified as monogamous or promiscuous following typical classifications of lamprologine mating systems^{22–24}. Specifically, species were considered monogamous if both the male and female typically mate with a single partner for a given reproductive effort, whereas species were considered promiscuous if either the male or the female concurrently mates with multiple partners. We then reconstructed the ancestral mating systems of cichlids at each of the five independent evolutionary transitions to cooperative breeding. Ancestral state reconstructions revealed no clear support for monogamous mating systems at any of the independent evolutionary transitions to cooperative breeding (Fig. 1). Indeed, one of the transitions to cooperative breeding (node 6 in Fig. 1) emerged from a promiscuous mating system, despite the high levels of within-group relatedness reported in *N. multifasciatus*²⁵, one of the cooperative species at this node. Next, to verify the pattern suggested by our ancestral state reconstruction (which showed that social and mating systems were not evolutionary coupled), we examined evolutionary correlations between social and mating systems across the phylogeny using Bayesian models of discrete character evolution. Once again, we found no support for the importance of monogamy as a necessary precursor of cooperative breeding, as there was no evolutionary correlation between mating system and evolutionary transitions to cooperative breeding across lamprologine cichlids (Fig. 2a, Table 1). Therefore, in contrast to other cooperatively breeding vertebrates^{1,4}, low ancestral levels of female promiscuity did not drive the evolution of cooperative breeding in cichlids.

The lack of coupling between monogamy and transitions to cooperative breeding in lamprologine cichlids allows us to resolve the

ongoing debate related to whether transitions to complex sociality influence intra-sexual selection^{17,18}. Because cooperatively breeding lamprologine cichlids did not evolve from monogamous ancestors, we evaluated the hypothesis that transitions to cooperative breeding alter the strength of intra-sexual selection and lead to a reduction in sexual dimorphism¹⁷, without the confounding effects of ancestral mating system obscuring our analysis. Consistent with expectations that cooperative breeding dampens sex differences, we found that cooperative breeding cichlids have reduced sexual size dimorphism relative to non-cooperative species (Fig. 3). These results provide clear evidence that cooperative breeding per se influences the evolution of sexual dimorphism.

We next tested the hypothesis that direct benefits drive the evolution of cooperative breeding in cichlid fishes²⁶. Predation risk represents a powerful selective force that influences behaviours and parental care strategies among Tanganyikan cichlids^{27,28}. Many lamprologine species are frequently depredated by piscivorous fish (oftentimes by piscivorous lamprologine species), which reduces adult and juvenile survival probabilities and promotes group living, biparental care and helping behaviours^{21,26,29,30}. Therefore, we hypothesized that evolutionary transitions to cooperative breeding occurred more frequently in species that gain anti-predator benefits through group membership and when biparental care is required to ensure offspring survival. Diet is also hypothesized to influence evolutionary transitions to cooperative breeding by influencing variation in resource availability⁷. Among lamprologine cichlids, food is less abundant and more temporally and spatially variable in piscivorous species compared to non-piscivorous species (for example, species with algal or planktonic diets), and piscivorous species exist at lower densities in Lake Tanganyika³¹. Therefore, we hypothesized that non-piscivorous diets facilitate cooperative breeding either by leading to habitat saturation and constraints on dispersal and independent breeding due to diet-mediated increases in population densities^{8,10}, or because abundant resources decrease the costs incurred by dominants of co-habiting with subordinate individuals, thereby facilitating social grouping³².

To evaluate these alternative hypotheses linked to the direct benefits of cooperation, we classified species based on their parental care system, social organization and diet. Species were classified as providing biparental care if both the male and female care for the offspring, and maternal care if only the female cares for the offspring (no species included in the current study provides sole paternal care). For social grouping, species were considered to group if they shoal or repetitively interact in groups³³, and were otherwise considered to be non-grouping. For diet, species were considered piscivores if they primarily hunt and eat other fish³⁴, and were otherwise considered non-piscivores. We then evaluated if each of these alternative hypotheses were evolutionary coupled with cooperative breeding. Indeed, we found support for evolutionary coupling of grouping, biparental care and non-piscivorous diets with the evolution of cooperative breeding, albeit to varying levels. Evolutionary transitions to cooperative breeding were very strongly coupled with social grouping and with parental care (Fig. 2b–d, Table 1, Supplementary Fig. 1), and were more likely to occur in group-living species, and in species with biparental care (Fig. 2b, c). Additionally, all 15 cooperatively breeding species for which we had diet data were non-piscivorous (Fig. 1), although Bayesian analyses demonstrated little evidence of co-evolution between diet and cooperation (Table 1, but also see the high transition rate to cooperative breeding associated with non-piscivory in Fig. 2d).

These results suggest that the evolution of cooperative breeding in fishes is promoted by ecological and life-history constraints that influence the direct benefits of cooperative behaviours. To visualize the relative influence, and control for potential evolutionary interactions among these variables, we conducted a *d*-separation phylogenetic path analysis (PPA). The best-supported PPA model

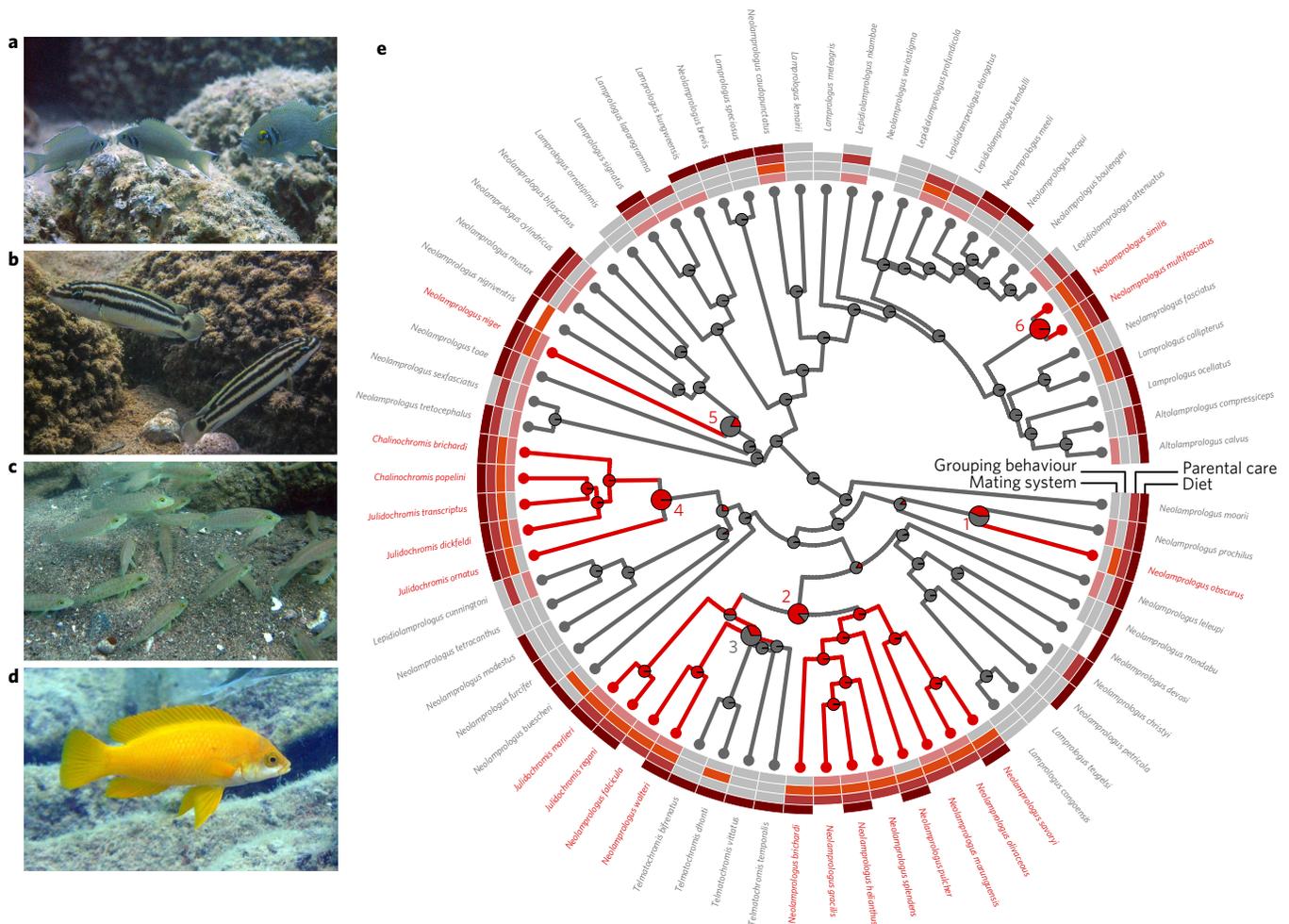


Figure 1 | Behavioural diversity in lamprologine cichlids. **a–d**, Lamprologine cichlids exhibit pronounced diversity in social and reproductive behaviours, including: obligate cooperative breeding, as seen in *N. pulcher* (**a**) and *J. ornatus* (**b**); social grouping without cooperative breeding and breeding promiscuously, as seen in *Lamprologus callipterus* (**c**); and socially monogamous pair bonds, as seen in *N. mustax* (**d**). **e**, Phylogenetic distribution of cooperative breeding in lamprologine cichlids and their associated behavioural and ecological traits. Grey and red species labels, branches and pie charts represent non-cooperative and cooperative species, respectively. Pie charts at each node represent Bayesian ancestral reconstructions of social systems. The five independent evolutionary transitions from non-cooperative to cooperative breeding and single loss of cooperative breeding are depicted using larger nodes labelled with red (nodes 1, 2, 4–6) and grey (node 3) numbers, indicating gains and losses of cooperative breeding, respectively, representing evolutionary nodal posterior probability values >0.75 in support of cooperative breeding. For transitions 1, 3, and 5 the nodal reconstruction could not unambiguously resolve the ancestral state, indicating that the evolutionary transition occurs along the branch. Mating system (red, monogamous; grey, promiscuous), grouping behaviour (red, social grouping (for example, groups of interacting individuals or shoals); grey, no social grouping); parental care system (red, biparental care; grey, maternal care) and diet (red, non-piscivore; grey, piscivore) are depicted in the concentric rings around the phylogeny from the innermost to outermost ring, respectively (note that various shades of red were used to assist in the interpretation of the figure; for detailed information on how species were classified see Supplementary Information). Unknown states are presented in white. Ancestral state reconstruction of mating systems at each of the six evolutionary transitions to cooperative breeding could not distinguish between monogamous or promiscuous ancestral states (transition number: posterior probability of monogamy, posterior probability of promiscuity; 1: 0.50, 0.50; 2: 0.52, 0.48; 3: 0.46, 0.54; 4: 0.53, 0.47; 5: 0.55, 0.45; 6: 0.10, 0.90). Photos: J. Desjardins (**a**), S. Marsh-Rollo (**b,d**) and J. Reynolds (**c**).

(Fig. 2e) shows that social grouping, parental care system and diet all directly influence the evolution of cooperative breeding, and that each of these relationships were in the direction predicted by the discrete analyses above. Additionally, both grouping and mating system have strong influences on parental care type (log odds ratio > 2, Fig. 2), with biparental care being more likely in monogamous, group-living species. Therefore, our path analysis provides no evidence for a direct relationship between monogamy and cooperative breeding in cichlids, and instead highlights the role of direct benefits as a key evolutionary driver in this system. Indeed, our evaluation of the evolutionary relationship among mating and parental care systems revealed that the most probable evolutionary pathway to becoming a monogamous, biparental species was

through initial transitions to promiscuous mating systems followed by secondary transitions to biparental care, at which point transitions to cooperative breeding become more probable, and finally by tertiary transitions to monogamy (Supplementary Figs 1, 2).

Our results provide a counterpoint to previous findings^{1,4–6} that ancestrally low levels of promiscuity promote evolutionary transitions to cooperative breeding. Instead, cichlids exhibit an alternative evolutionary path to cooperative breeding, one in which kin-selection appears to not be the primary driver of evolutionary transitions to cooperative breeding. Although we cannot rule out the possibility that cooperative breeding cichlids receive indirect benefits, because ecological factors promote kin-structured populations¹², the available evidence suggest this is an unlikely explanation

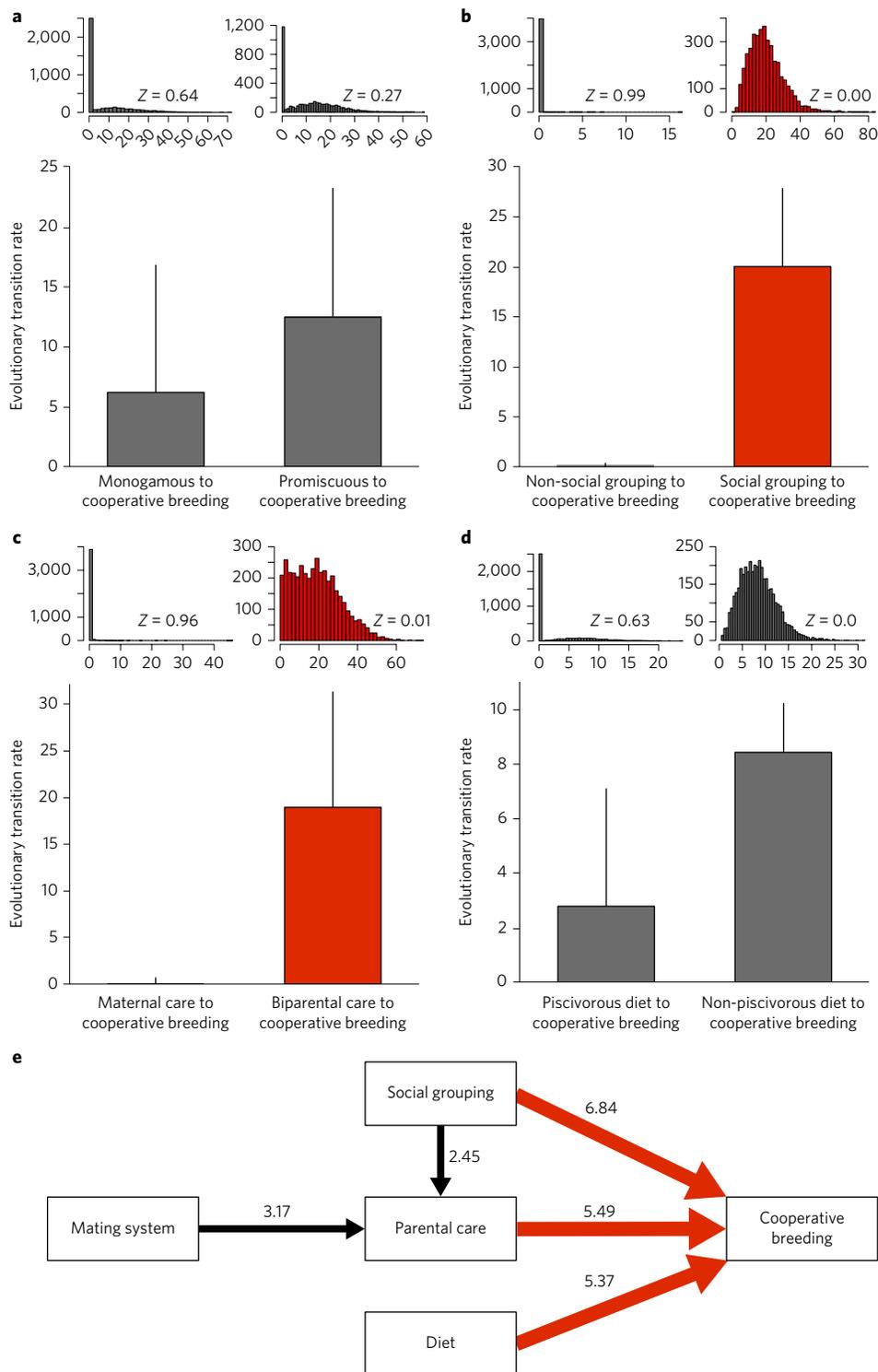


Figure 2 | Evolutionary drivers of cooperative breeding in lamprologine cichlids. a-d, Mean evolutionary transition rates ($q_{xy} + s.d.$) derived from the Bayesian models of discrete character evolution, which indicates the likelihood of a transition occurring, between mating system (**a**, monogamous versus promiscuous), social grouping (**b**, non-grouping versus grouping), parental care (**c**, maternal versus biparental) and diet (**d**, piscivore versus non-piscivore), and evolutionary transitions to cooperative breeding. Histograms show 4,000 samples from the posterior distribution of evolutionary transition rates, with rate transition parameters on the x axis and frequency on the y axis. Transition rates that are rarely assigned to zero ($Z \leq 0.05$) are considered probable evolutionary events. Probable transitions are presented in red and unlikely transitions are presented in grey. Although transitions from non-piscivorous diets to cooperative breeding appear likely, we conservatively coded this transition as unlikely as there was weak evidence for an evolutionary coupling of diet and cooperative breeding (see Table 1). Here, we only present evolutionary transitions to cooperative breeding, however, complete evolutionary transition diagrams are presented in the Supplementary Fig. 1. **e**, Best model from d -separation phylogenetic path analysis of the causal relationship among traits related to the evolution of cooperative breeding in cichlids. Arrows indicate direct relationships between variables in the model, with the size of the arrow being scaled to the magnitude of the standardized path coefficient (which is also labelled for each direct relationship). Red arrows indicate evolutionary transitions to cooperative breeding.

Table 1 | Bayesian discrete analysis of correlated evolution with cooperative breeding.

Trait	Dependent model	Independent model	\log_{10} Bayes factor
Mating system	-73.88	-75.49	0.698
Grouping	-49.39	-63.03	5.921
Parental care	-61.73	-74.77	5.663
Diet	-52.63	-54.22	0.688

The smoothed estimate of the maximum likelihood for the dependent and independent models of evolution, as well as the \log_{10} Bayes factor, for the correlated evolution of mating system (monogamy versus promiscuous), social grouping (non-grouping versus grouping), parental care system (maternal versus biparental), and diet (piscivore versus non-piscivore) with cooperative breeding (cooperatively breeding versus non-cooperatively breeding) in lamprologine cichlids. Larger \log_{10} Bayes factor values indicate strong support whereby values of <1 indicate weak evidence, 1–2 indicate strong evidence and >2 indicate decisive evidence.

for the evolution of cooperative breeding. For example, in the well-studied cooperatively breeding cichlid *N. pulcher*, individuals appear to preferentially disperse away from relatives³⁵. Additionally, the available evidence suggests that cooperatively breeding cichlids typically form social groups with low relatedness³⁶, although further characterization of within-group relatedness in cooperatively breeding cichlids is required to validate if this is indeed the most common pattern across cooperative species. Instead, our findings suggest that cooperative breeding in cichlids may have evolved in response to direct fitness benefits.

The contrast in our results and those of previous studies^{1,4–6} could represent a fundamental difference in the mechanisms favouring cooperative breeding among fish versus other taxa. Cichlids do not typically provision offspring with food (a key alloparental behaviour in other taxa), and fish fecundity increases with age, which could influence the costs of delaying sexual maturation and helping. Moreover, relatively short life spans (compared to cooperatively breeding birds and mammals) and predation-mediated rapid breeder turnover may prevent the formation of closely related family groups, thereby reducing potential indirect benefits gained by helping³⁷. Regardless, our findings suggest that an increased focus on the benefits and costs of cooperative behaviour (that is, the ‘*b*’ and ‘*c*’ in Hamilton’s rule), rather than just on the co-efficient of relatedness (*r*), will provide a more comprehensive understanding of the evolution of complex sociality.

Methods

Data collection. We collected binary data on social system, mating system, parental care system, social grouping and diet for 69 of the approximately 80 lamprologine species from the literature (see Supplementary Table 1). For cooperative breeding, species were considered cooperative if they form permanent social groups with subordinate helpers⁴, and otherwise they were considered non-cooperative. In most cooperatively breeding cichlids studied to date, helpers have low levels of within-group relatedness, although relatedness values can vary widely (for example, *N. pulcher*, *N. savoryi*, *J. ornatus*^{38–41}). This pattern of relatedness seems to be common among cooperative cichlids, however in at least two other cooperative species helpers are highly related to dominant breeders (*N. multifasciatus* and *N. obscurus*^{25,42,43}). Species were classified as monogamous or promiscuous following typical classifications of the lamprologine mating system^{22–24} (monogamous, males and females typically mate with a single partner; promiscuous, either the male or female mates with multiple partners during a single reproductive period). Species were classified as promiscuous either if males were polygynous or if females were polyandrous—see also ‘Sensitivity testing’ below, where we use alternative classifications of mating systems. Also following typical classifications of lamprologine cichlids^{22–24}, species were classified on the basis of their parental care system (biparental care, both males and females care for the offspring; maternal care, only the female cares for the offspring), social grouping (grouping species, species that shoal or repetitively interact in groups³³; non-grouping species, species that do not shoal or repetitively interact with conspecifics). For diet, species were considered piscivores or non-piscivores³⁴ (piscivores, species that primarily hunt and eat other fish; non-piscivores, species that do not specialize on eating other fish).

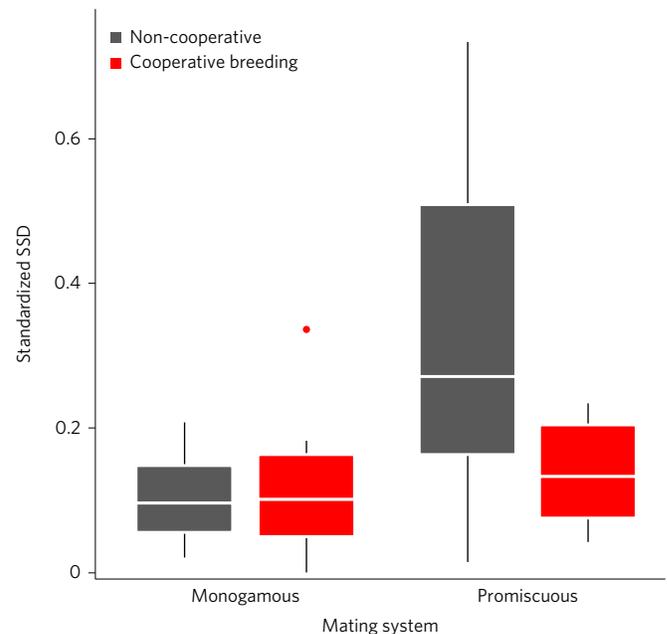


Figure 3 | Contrasting sexual size dimorphism between social and mating systems in lamprologine cichlids. As expected, sexual size dimorphism (SSD) is lower in monogamous than promiscuous species (posterior mean: -0.21, 95% confidence interval (CI) (-0.98, -0.09), $P_{\text{MCMC}} = 0.005$). Furthermore, cooperative breeding species have reduced sexual size dimorphism relative to non-cooperative species (posterior mean: -0.21, 95% CI (-0.38, -0.07), $P_{\text{MCMC}} = 0.014$), and this effect is greater for species with promiscuous mating systems (social system:mating system interaction, posterior mean = 0.23, 95% CI (0.00, 0.45), $P_{\text{MCMC}} = 0.045$). The median value is indicated with a white line in each box plot with the 25th and 75th percentiles forming the lower and upper limits of the box and the line indicating the 10th and 90th percentiles. Sample sizes for each box are 10, 7, 14 and 7 (from left to right, respectively).

To test the hypothesis that there is reduced sexual size dimorphism in cooperatively breeding species we compiled mean standard length data for males and females of 38 species of lamprologine cichlids (14 cooperatively and 24 non-cooperatively breeding species). Most of this data ($n = 25$) came from collection of wild-caught, sexually mature individuals collected from a long-term field site located in Kasakalawe Bay, southern Lake Tanganyika (8° 46' 52" S, 31° 5' 18" E) in 2004, 2005, 2008 or 2013. Methods used to sample wild-caught fish conformed to protocols approved by the Animal Research Ethics Board of McMaster University, adhere to the Canadian Council for Animal Care guidelines, and were conducted with the cooperation and permission of the Zambian Department of Fisheries.

We combined our field-collected data with data on male and female standard length obtained from the literature for 13 species. Literature data was also available for eight additional lamprologine cichlid species for which we lacked field-collected data. We took the weighted averages from all sources as our final value whenever possible (see Supplementary Table 1). When field data was not available we used records from aquarist data. We were able to find aquarist data for five additional species, all of which were cooperative breeders (see Supplementary Table 1). However, to verify the validity of using aquarist records, we collected additional data from aquarist records for 22 species (8 cooperatively and 14 non-cooperatively breeding species; see Supplementary Table 2) for which we already had field data, and compared the aquarist records with data collected from the field. We determined that aquarist records overestimate the size of both males (paired *t*-test $t_{21} = 7.58$, $P < 0.001$) and females (paired *t*-test $t_{21} = 4.34$, $P < 0.001$). However, the overestimation is relatively higher for male than for female fish, and aquarist records therefore consistently overestimate the degree of sexual size dimorphism (paired *t*-test $t_{21} = 3.98$, $P < 0.001$). Because all the species for which we had aquarist data only were cooperative breeders, including these data would only dampen our ability to test the hypothesis that cooperative breeders have reduced sexual dimorphism¹⁷, and we therefore included these data in our final dataset (Supplementary Table 2).

Phylogeny. Numerous studies, which have evaluated the evolutionary relationships among lamprologine cichlids, have shown cases of introgressive hybridization among species^{20,44–50}. These studies have also shown that mitochondrial DNA

(mtDNA) is more prone to introgression than nuclear DNA (nDNA), leading in an extreme case to complete unidirectional transfer of mtDNA between species⁴⁸. Therefore, to generate a robust phylogeny that accounts for the evolutionary history of introgression in lamprologine cichlids we identified known cases of introgression and incorporated this information into our tree-building procedures.

We used five nuclear genes (recombination-activating gene 1 exon 3 (rag1), ribosomal protein S7 exon 1–2 (S7-1), ribosomal protein S7 intron 2 (S7-2), 18S ribosomal RNA internal-transcribed spacer 1–2 with 5.8S and 28S ribosomal RNA partial sequences (ITS), large subunit ribosomal RNA (LSU)) and three mitochondrial genes (NADH dehydrogenase subunit 2 (ND2), the mitochondrial control region (control), cytochrome B (CytB)) to construct a phylogeny for 69 lamprologine cichlids. Nuclear genes are more robust to introgression than mitochondrial genes, as nuclear-derived topologies are consistent with morphological and behavioural groupings of species²⁰. Geneious 7.0.4 (Biomatters, 2013) was used to search the National Center for Biotechnology Information (NCBI) database for sequences (see Supplementary Table 3 for accession numbers). We excluded mtDNA from three species (*N. similis*, *N. multifasciatus* and *N. fasciatus*), where mitochondrial sequences are clearly affected by introgression^{47,48} and used nDNA exclusively for these species during the phylogeny building procedures. Gene sequences were aligned using MUSCLE⁵¹ and uploaded in MESQUITE⁵² v2.75 for visual inspection of alignments. For each gene we used jModelTest⁵³ v2.1.6 to assess three substitution models to determine the best-fit model of nucleotide substitution based on a sample-size-corrected Akaike Information Criterion. The best-fit nucleotide substitution models, which were subsequently used during phylogeny construction, were HKY for ITS, LSU and S7-1; HKY+Γ for S7-2; HKY+I for Rag1 intron 2, GRT+I for Rag1 exon 3 and GTR+Γ+I for ND2, the control region and CytB. However, owing to problems with convergence of the Bayesian chain for Rag1 exon 3 using the jModelTest best-fit model, we simplified the nucleotide substitution model to HKY for this sequence, which facilitated convergence.

Aligned sequences were uploaded into Bayesian phylogeny building software BEAUTi v1.6.2 and BEAST⁵⁴ v1.8.1. Within BEAUTi we incorporated information from a previously described lamprologine phylogeny²⁰, which represents the most robust and species-rich lamprologine phylogeny to date and which identified placement inconsistencies potentially caused by introgression, by comparing nuclear and mitochondrial phylogenetic topologies. Following ref. ²⁰, we assigned the *Telmatochromis* species group and the *Neolamprologus* species with brood care helpers as two distinct monophyletic groups and treated the paraphyletic groups from the *Julidochromis/Chalinochromis* complex as two separate monophyletic groups. The phylogeny was built using unlinked substitution models for each gene, a relaxed uncorrelated lognormal clock, and Yule speciation process, with priors set to a normal distribution with an initial value of 0.02 and upper and lower values of 1 and 0, respectively. The Markov chain Monte Carlo (MCMC) simulation chain length was set to 60 million with parameters sampled every 10,000 iterations. Stationarity was verified using Tracer⁵⁵ v1.6 software on the basis of examination of effective sample sizes (ESS) for each parameter and inspection of posterior distribution traces. A maximum clade credibility (MCC) phylogeny was generated using a burn-in of 10% and a posterior probability limit of 0.95 using TreeAnnotator⁵⁴ v1.8.1. To verify the topology of the resulting phylogeny, we re-ran the procedures detailed above using alternative starting points and reproduced the same tree topology.

Ancestral state reconstruction. We reconstructed ancestral states of social and mating system using the MRCA implemented in the Multistate package in the program BayesTraits⁵⁶. In all cases the MCMC chain ran for 4,000,000 iterations following a burn-in of 1,000,000 iterations. The reversible jump hyperprior values (0–10) were set to ensure adequate mixing and model acceptance rates. Node numbers were identified using the node.label function in the ape⁵⁷ package in R⁵⁸, whereas descendant taxa from each node were identified using the phytools⁵⁹ package. Ancestral state probabilities for each character state were compared among nodes.

Discrete evolutionary correlations. We analysed the evolutionary correlations between cooperative breeding and behavioural, life-history and ecology traits predicted to influence the evolution of cooperative breeding (that is, mating system, parental care system, social grouping and diet) by using Bayes factors to compare the fit of dependent (that is, evolutionarily coupled) and independent models of trait evolution (Supplementary Fig. 1). Because there is potential covariance among mating system, parental care system, social grouping and diet, we also evaluated the relationships among these variables (Supplementary Fig. 2, Supplementary Table 4). Bayesian MCMC analyses account for any phylogenetic uncertainty by estimating a parameter of interest across a sample of trees^{60,61}. Therefore, we used a reversible-jump Bayesian Markov chain Monte Carlo (RJ MCMC) analysis to derive posterior probability distributions of the independent and dependent models of character evolution and the model parameters to find the most probable evolutionary model⁶². The independent model of evolution assumes there is no correlation between the two traits being analysed, and that they evolve independently. The dependent model of evolution describes the evolution of a trait being dependent on the evolution of another trait, with eight possible transitions between the four character states of the two

dependent traits (Supplementary Figs 1–4). If the dependent model of evolution is favoured, the Bayesian MCMC analysis can be used to find which of the eight transitions are most supported and thus identify the most probable direction of evolutionary causality between character states.

Every 10th tree from the 10,000 tree output from the MCC phylogeny was taken, reducing it to a sample of 1,000 trees for analysis in BayesTraits. Both independent and dependent models of evolution were analysed using RJ MCMC analysis. For Bayesian MCMC analysis methods, parameters have to be set for analysis, with particular care taken when setting prior distributions⁶². Here, hyper priors were chosen as they use the data to estimate details of the prior distribution, therefore reducing some of the uncertainty associated with choosing priors. Because BayesTraits does not summarize the results of the MCMC analysis, these outputs were uploaded into Tracer⁵⁵ for analysis. Reverse-jump hyper prior values of (0–10) were selected to ensure ESS acceptance rates >200 for all models. The same number of iterations were used for each analysis (5 million) with a burn-in of 1 million used for each analysis to avoid including values before convergence of the Markov chain⁶².

Log₁₀ Bayes factors were calculated in Tracer for each pair of models⁵⁵, on the basis of a bootstrapping procedure used to estimate marginal likelihoods^{63,64}. In this case, the Bayes-factor value shows the weight of evidence to support the dependent model of evolution over the independent model, with values from <1 indicating little evidence, 1–2 strong evidence and >2 decisive evidence⁶⁵ for the dependent over the independent model. Z scores were calculated for each transition parameter. These are calculated by finding out how many of the transition rates are zero, across the sample of trees. The Z score is important as it provides support for the posterior probability of a selected transition. The posterior probability distribution gives a distribution of the likelihood of a transition occurring. The more times a transition is assigned a number other than zero (Z), the more the posterior probability distribution will shift away from zero and become more likely. Likewise, the higher the average of the posterior probability distribution (the average posterior probability), the more the distribution is shifted away from zero, and the more supported the evolutionary transition. Therefore a high average posterior probability and a Z score of 0 would show high support for a transition. Both the Z scores and average posterior probabilities of each transition were therefore used to find the most probable evolutionary transitions between the four character states of the two traits of each analysis⁶². The Multistate module within BayesTraits⁵⁶ was used to determine the ancestral states of the most recent common ancestors of each cooperative lineage from the consensus tree, and all models were run using fossilized roots to the most probable ancestral state—however assessing models without fossilized roots did not qualitatively change the results (see ‘Sensitivity Testing’ below).

Sexual dimorphism. To test the hypotheses that intra-sexual selection is similar between the sexes in cooperatively breeding cichlids^{17,66,67}, we used a Bayesian MCMC generalized linear mixed model to compare sexual size dimorphism between cooperative and non-cooperative species, implemented in the MCMCglmm⁶⁸ package in R⁵⁸. This method allows the inclusion of a phylogeny as a design matrix, to account for shared variance due to relatedness among species. Because some species in our dataset had larger females than males, and cooperative breeding is predicted to decrease the degree of sexual size dimorphism, we used the absolute value of sexual size dimorphism (absolute ((log(male standard length) – log(female standard length))) as the response variable. However, models run with the raw value of sexual size dimorphism gave qualitatively similar results. The fixed effects included in the model were the binary scores of social system (cooperative/non-cooperative), mating system (monogamous/promiscuous) and their interaction. Species was included as a random effect. We used the prior (list (G = list (G1 = list (V = 1, nu = 0.02)), R = list (V = 1, nu = 0.02))), which is equivalent to an inverse-Gamma distribution with a shape and scale parameter of 0.01. The MCMC algorithm was run for 1,000,000 iterations, with a burn-in of 50,000 and a sampling interval of 500.

Phylogenetic path analysis. We used the phylogenetic *d*-separation method^{69–71} to test models of the relationships among five variables related to the evolution of cooperative breeding in lamprologine cichlids. The variables used were the binary scores of (1) cooperative breeding, (2) mating system, (3) parental care, (4) diet and (5) grouping, described in the main text. We built 12 biologically relevant models (Supplementary Fig. 5) based on the hypothesized relationships among variables that had been suggested in previous studies^{1,4,8,19,72–74}, and from the discrete analysis conducted in this study. These models were constructed as directed acyclic graphs, which are required for this type of analysis. Each model was then converted to a set of conditional independencies (see ref. ⁷¹ for details), which were tested using phylogenetic binary regression models in the ape⁵⁷ package in R⁵⁸ and the consensus tree produced in this study. Using these phylogenetic logistic regression models, we calculated Fisher's *C*-statistic and the *C*-statistic Information Criterion⁷⁵ (CICc) for each conceptual model to facilitate model selection. After selecting the best model (lowest CICc score), we calculated standardized path coefficients using phylogenetic logistic regressions.

Comparison of models based on CICc values indicated that model F was the best model (Supplementary Table 5, evidence ratio with next best model = 3.00).

This model, and the next four best models, all include a direct causal influence of parental care, social grouping and diet on the evolution of cooperative breeding, consistent with the analyses presented in the main text. However, models without any causal links among parental care, mating system, grouping and diet (that is, model A, B) performed poorly, demonstrating the importance of considering indirect influences on the evolution of cooperative breeding (and on evolutionary phenomena in general). Additionally, models with a direct causal influence of mating system on cooperative breeding (A and L) had a poorer model fit than similar models without this influence (B and F), suggesting that mating system does not have a direct influence on the evolution of cooperative breeding in cichlids. While model L appears to be competitive with the best model ($\omega\text{CICc} = 0.09$), visual comparison of these two models shows they contain the same causal relationships among the variables, with the exception of one additional link in model M (from mating system to cooperation). The addition of single, uninformative link will cause a marginal increase in CICc scores, and will therefore appear to create competitive models, however in such cases the simpler model should be preferred⁶. Indeed, after controlling for diet, grouping and parental care, mating system has a weak and non-significant influence on cooperative breeding (phylogenetic binary regression: $\log\text{-odds} \pm \text{s.e.} = -0.16 \pm 0.83, P = 0.85$).

Sensitivity testing. The discrete evolutionary correlation analyses presented in the main text were conducted using roots that were fossilized to the most probable ancestral state, determined using the Multistate function in BayesTraits. However, we also ran equivalent analyses with non-fossilized roots to ensure our results were robust to this decision. Using non-fossilized roots altered the most probable ancestral state for the analysis of co-evolution between cooperative breeding and diet, suggesting that the common ancestor of this clade was non-piscivorous. However, using non-fossilized models did not qualitatively change the weight of evidence (Bayes factors) for the evolutionary correlations between traits (Supplementary Table 6) compared to the analyses using fossilized roots presented in the main text. Additionally, transitions to cooperative breeding were still more probable in species with biparental care, social grouping and non-piscivorous diets (Supplementary Fig. 3).

Additionally, for two species, there was some uncertainty in the literature whether the species is cooperative or non-cooperative (see Supplementary Table 1). For the analyses presented in the main text, we used the most conservative classification of cooperative breeders, such that any species where there is uncertainty in the social system was considered non-cooperative (see Supplementary Table 1). However, to determine whether variation in the definition of cooperation influenced the results of the discrete analyses, we also used the most liberal classification of cooperative breeders, such that any species where there is uncertainty was considered cooperative (Supplementary Fig. 4). Further, in the main text we classified species as either classically monogamous or promiscuous (including, polygyny, polyandry or polygynandry). However, because female monogamy influences within-group relatedness to a greater extent than male monogamy, and increased within-group relatedness is one of the primary arguments for monogamy driving the evolution of cooperation^{1,4,6}, we also conducted additional analyses considering female mating system (that is, whether the females are monogamous or promiscuous, regardless of male mating system), rather than using a classical mating system (Supplementary Table 7). For five species, there was some uncertainty in the literature whether the females were monogamous or promiscuous, and so we conducted the analyses using both the most conservative classification (that is, any species with uncertain mating system classification was considered monogamous) and the most liberal classification of female mating system (that is, any species with uncertain mating system classification was considered promiscuous). The results of analyses conducted using alternative classifications of social system, or mating system, were largely similar to those reported in the main text (Supplementary Fig. 4, Supplementary Table 7). Transitions to cooperative breeding were still more probable in species with social grouping and with non-piscivorous diets (Supplementary Fig. 4). In contrast to the main analysis, models conducted with the alternative classification of cooperation produced strong evidence that transitions to cooperative breeding were dependent on diet (\log_{10} Bayes factor = 1.07, Supplementary Table 7). Additionally, all analyses conducted using alternative classifications produced models with no substantial support for a relationship between cooperation and mating system, and strong evidence for a dependent relationship between cooperation and ecological variables (Supplementary Table 7).

Relationships among independent variables. We determined in our primary analyses that mating system has a weaker evolutionary correlation with cooperative breeding than parental care, grouping or diet (Table 1, Fig. 2). When we looked at the relationships among mating system, parental care, grouping and diet, we found that mating and parental care were very strongly evolutionarily correlated (Supplementary Fig. 2, Supplementary Table 4), with monogamy and maternal care being an evolutionary unstable state (Supplementary Fig. 2a). Further, we found very strong evidence for a relationship between parental care and grouping (Supplementary Table 4), with social grouping and maternal care being an evolutionary unstable state (Supplementary Fig. 2d).

Data availability. Data used in this study are available in Supplementary Tables 1–3.

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Author contributions

C.J.D., C.M.O., S.S., S.B. and J.L.F. conceived the study; C.M.O., H.W., S.B. and J.L.F. collected the data; C.J.D., C.M.O., H.W., S.S. and J.L.F. analysed the data; C.J.D., C.M.O., S.B. and J.L.F. wrote the paper with input from the other authors.

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The authors declare no competing financial interests.