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What is cooperative breeding in mammals and birds? Removing definitional barriers for comparative research

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ABSTRACT

Cooperative breeding (i.e. when alloparents care for the offspring of other group members) has been studied for nearly a century. Yet, inconsistent definitions of this breeding system still hamper comparative research. Here, we identify two major inconsistencies, discuss their consequences and propose a way forward. First, some researchers restrict the term 'cooperative breeding' to species with non-breeding alloparents. We show that such restrictive definitions lack distinct quantitative criteria to define non-breeding alloparents. This ambiguity, we argue, reflects the reproductive-sharing continuum among cooperatively breeding species. We therefore suggest that cooperative breeding should not be restricted to the few species with extreme reproductive skew and should be defined independent of the reproductive status of alloparents. Second, definitions rarely specify the type, extent and prevalence of alloparental care required to classify species as cooperative breeders. We thus analysed published data to propose qualitative and quantitative criteria for alloparental care. We conclude by proposing the following operational definition: cooperative breeding is a reproductive system where >5% of broods/litters in at least one population receive species-typical parental care and conspecifics provide proactive alloparental care that fulfils >5% of at least one type of the offspring's needs. This operational definition is designed to increase comparability across species and disciplines while allowing to study the intriguing phenomenon of cooperative breeding as a behaviour with multiple dimensions.

Key words: alloparental care, cooperative breeding, communal breeding, birds, mammals, definition, helping, breeding monopolisation, reproductive skew, comparative research.

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I. INTRODUCTION

Cooperative breeding can be tentatively defined here as a breeding system where more than two individuals provide parental care to the offspring of conspecifics (see Table 1 for key examples of definitions used in the literature and see Table S1 in the online Supporting Information for a complete list). This phenomenon has attracted much research interest during the last century (e.g. Skutch, 1935; Camerlenghi *et al.*, 2022) as it apparently challenges the Darwinian notion of individual fitness and has fundamental links to diverse biological questions, including the evolution of cooperation (e.g. Zahavi & Zahavi, 1997; Burkart *et al.*, 2014), communication (e.g. Leighton, 2017), social behaviour (e.g. Ben Mocha, Mundry & Pika, 2018) and physiology (e.g. menopause: Lahdenperä *et al.*, 2004). Cooperative breeding has therefore been studied in a variety of disciplines, including behavioural ecology, physiology and comparative psychology.

In addition, it has been argued that humans are a cooperatively breeding species (Hrdy, 2007; Burkart, Hrdy & van Schaik, 2009) and that this trait played a distinctive role in human physiological, social and cognitive evolution (Hill & Hurtado, 2009; Tomasello & Gonzales-Cabrera, 2017). Comparative research on the causes and consequences of cooperative breeding is therefore important to shed further light on the evolution of our species (Burkart *et al.*, 2009; Isler & van Schaik, 2012).

While multidisciplinary research has contributed important and different perspectives on cooperative breeding, this has come at the cost of inconsistencies that hinder valid comparisons among taxonomic groups, studies and disciplines (Sherman *et al.*, 1995; Pruett-Jones, 2004). Foremost, comparative studies often classify species in a binary manner as cooperative or non-cooperative breeders according to a specific definition, and use this list of classified species as a predictor or response variable in their analyses (e.g. Jetz & Rubenstein, 2011; Leighton, 2017). Hence, if comparative studies use different operational definitions, the same group of species will be classified differently and the results of these studies will not be comparable.

Our review aims to advance comparative research of cooperative breeding by providing a unifying definition for this phenomenon. To this end, we first identify two primary sources of inconsistencies in common definitions of cooperative breeding. Next, we demonstrate how these inconsistencies hinder comparisons among studies, and suggest evidence-based solutions to each. We conclude by proposing an operational definition to be used across disciplines and discuss its advantages for understanding the evolution of cooperative breeding.

(1) Definitions of cooperative breeding

We reviewed definitions for cooperative breeding published since 1974 in the fields of ornithology, mammalogy and evolutionary anthropology [see Tables 1 and S1, and Solomon & French (1997) for an earlier historical account]. We focused on theoretical and comparative studies because they often present cross-species definitions.

Although the various definitions show much overlap (see Table S1), two primary sources of inconsistencies were identified. First, definitions vary regarding whether cooperative breeding should be restricted to species with non-breeding helpers, or whether it should also include species where reproduction is shared, albeit unequally, among group members (Solomon & French, 1997; Burkart *et al.*, 2009). Second, definitions rarely set criteria regarding the required (*i*) type and extent of alloparental care and/or (*ii*) the prevalence of cooperative breeding groups within a population.

II. INCONSISTENCY PROBLEM I: SHOULD COOPERATIVE BREEDING BE RESTRICTED TO SPECIES WITH NON-BREEDING HELPERS?

Most theoretical and comparative studies used inclusive definitions in which alloparental care can be provided by breeding and/or non-breeding helpers (Table 1). However, some comparative studies adopted restrictive definitions that limit cooperative breeding to species where alloparental care is provided partly (e.g. Ligon & Burt, 2004), or even solely (e.g. Blumstein & Armitage, 1999; Clutton-Brock, 2006), by alloparents that do not breed while helping. Proponents of this restrictive approach divide species with alloparental care into cooperative breeders where alloparental care is provided by non-breeding helpers, and communal breeders where alloparental care is provided by breeding and non-breeding members of the social unit (Solomon & French, 1997; Clutton-Brock, 2006).

Table 1. Examples of definitions of cooperative breeding used in theoretical and comparative studies in ornithology, mammalogy and evolutionary anthropology since 1974. Examples were chosen to represent the diversity of different criteria (see Table S1 for the full list of reviewed definitions).

Definition	Theoretical/ operational[1]	Restrictive/ inclusive[2]	Required type of alloparental care	Required prevalence of cooperative breeding groups in a population	Discipline & Reference
'Reproductive system in which one or more members of a social group provide care to young that are not their own offspring. The aid-givers may be non-breeding adults, in which case they are usually called "helpers" or "auxiliaries", or they may be co-breeders, and share reproduction with other group members of the same sex'.	Theoretical	Inclusive	'Although the care given usually includes providing food, it may involve other parental-type behaviours as well, including territorial defense, nest or den construction, incubation and defense against predators'	Not defined	Ornithology Stacey & Koenig (1990, p. ix)
'Cooperative breeding was assigned where a reasonable proportion of broods in at least one population are provisioned by more than two individuals… In general in cooperative species helpers attend more than 10% of nests'	Operational	Inclusive	Not defined	>10%	Ornithology Cockburn (2003, p. 2208)
'We only classed species as cooperative if helpers did not breed or had zero-to-limited opportunities to breed; typically, these helpers would be retained natals […] We did not define species as cooperative unless there were helpers present in at least 10% of the nests in any part of their range'	Operational	Restrictive	Not defined	≥10%	Ornithology Cornwallis *et al.*, (2010, 'methods section')
'An individual that helps in the raising of conspecific offspring that are not their own, often while foregoing their own reproduction'	Operational	Inclusive	Not defined	Not defined	Ornithology Griesser & Suzuki (2016, p. 3)
'Cases where more than a pair of individuals exhibit helping behaviour towards young from a single litter, or where individuals assist the breeding pair'	Theoretical	Inclusive	'Any activity directed towards infants or their parents which is likely to benefit the recipients and increase breeding success (e.g. alarm calling or provisioning a pregnant female) […]. We suspect, however, that workers are most interested in a subset of costly helping behaviours – those which appear to decrease the donor's direct fitness relative to that it would possess if it did not perform these activities'	Not defined	Mammalogy Jennions & Macdonald (1994, p. 90)
'We include species as cooperative breeders only if a proportion of females do not breed regularly and show alloparental care…'	Operational	Restrictive	'Alloparental care (such as contributing to provisioning or carrying young born to other females)'	Not defined	Mammalogy Lukas & Clutton-Brock (2012*a*, p. 2151)
'A breeding system in which group members other than the genetic parents (alloparents) help one or both parents care for and provision their offspring'	Theoretical	Inclusive	'Care for and provision their offspring'	Not defined	Evolutionary anthropology Hrdy (2007, p. 40)

[1]We differentiate between definitions presented in theoretical studies and operational definitions that were used to classify species in a comparative study because the latter definitions were used to classify species and may therefore be more robust.
[2]Restrictive definition = species are cooperative breeders only when helpers are mostly or completely do not reproduce themselves; inclusive definition = species are cooperative breeders regardless of the breeding status of helpers.

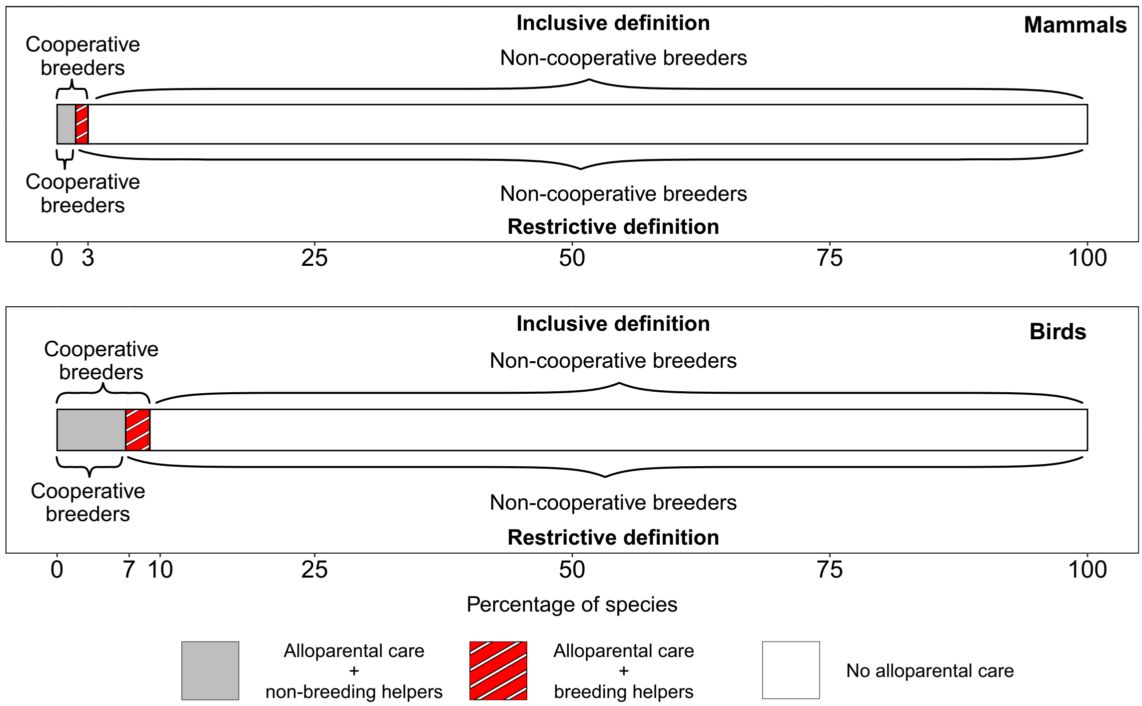

Fig. 1. Quantitative differences in the binary classification of mammal and bird species as cooperative *versus* non-cooperative breeders according to inclusive/restrictive definitions of cooperative breeding (i.e. species with breeding/non-breeding helpers). The top row shows the percentages of mammal species exhibiting alloparental care by non-breeding helpers (1.8%), alloparental care by breeding helpers (1.2%) and species without alloparental care (97%) (Lukas & Clutton-Brock, 2012*a*). The bottom row shows the percentages of bird species exhibiting alloparental care by mostly non-breeding helpers (6.7%), alloparental care by breeding helpers (2.3%) and species without alloparental care (91%) from Riehl (2013). Note that Riehl (2013) argued for a continuum of reproductive sharing among cooperative species rather than a categorical separation, and hence these values are estimates.

The decision on whether to use an inclusive or restrictive definition for the binary classification of species (i.e. cooperative/non-cooperative breeding) may significantly affect the outcome of comparative studies because communal breeders constitute a substantial proportion of the species exhibiting alloparental care in mammals (24/58 species = 41%; Lukas & Clutton-Brock, 2012*a*) and birds (55/213 species = 26%; Riehl, 2013) (Fig. 1). Nevertheless, communal breeding species are considered cooperative breeders in some analyses [often in ornithology (e.g. Jetz & Rubenstein, 2011; Leighton, 2017)], but as non-cooperative breeders in others [often in mammalogy (e.g. Lukas & Clutton-Brock, 2012*a*; Federico *et al.*, 2020)].

Inconsistency in applying inclusive or restrictive definitions of cooperative breeding hampers comparison across studies and taxonomic groups as demonstrated in the following example. Lukas & Clutton-Brock (2017) and Jetz & Rubenstein (2011) investigated the relationships between the same climatic factors and the distribution of cooperative breeding in mammals and birds, respectively. In mammals, only mean annual rainfall was found to affect the distribution of cooperative breeding, while in birds, additional climatic factors were found to have explanatory power (e.g. high between-year variation in precipitation). However, while a restrictive definition for cooperative breeding was used for mammals (i.e. considering only species with alloparental care and non-breeding female helpers), an inclusive definition was used for birds (i.e. considering species with alloparental care regardless of whether helpers breed or not). Consequently, it is unclear whether the dissimilarity between the results of these studies reflects a real difference between taxonomic groups or if this dissimilarity is due to the different definitions of cooperative breeding used to classify species.

(1) Abolishing the restrictive definition of cooperative breeding

Evidence-based proposals about whether the definition of cooperative breeding should be restricted to species with non-breeding helpers or not are crucial to advance comparative research of this breeding system. We suggest abandoning the restrictive approach to define cooperative breeding. Below, we present methodological and biological arguments for this suggestion while using as examples two restrictive definitions that were used to classify large data sets of mammals (Lukas & Clutton-Brock, 2012*a*) and birds (Cornwallis *et al.*, 2010).

Our methodological critique concerns quantitative ambiguities concerning the term 'non-breeding helpers'. Although being a key term in restrictive definitions, these definitions fail to define non-breeding helpers in distinct quantitative terms (Tables 1 and S1; see also Sherman *et al.*, 1995).

Table 2. Overlap between data sets classifying the same mammal and bird species as cooperative breeders or not (disagreements/agreements are marked in red/green, respectively).

	Mammals (*N* = 37 species; see Table S2 for details)			Birds (*N* = 28 species; see Table S3 for details)		
		Cooperative breeder (Lukas & Clutton-Brock, 2012*a*)	Not cooperative breeder (Lukas & Clutton-Brock, 2012*a*)			Number of cooperative species with helpers that 'did not breed or had zero-to-limited opportunities to breed' (Cornwallis *et al*., 2010)
Number of species (percentage)	Cooperative breeder (Lukas & Clutton-Brock, 2017)	29 (78%)	6 (16%)	Number of cooperative breeding species where subordinate females produce <10% of offspring (Raihani & Clutton-Brock, 2010)	Yes	22 (79%)
	Not cooperative breeder (Lukas & Clutton-Brock, 2017)	2 (6%)	0 (0%)		No	6* (21%)

*In these six species there is also no male reproductive monopolisation: common moorhen *Gallinula chloropus* (McRae, 1996); Mexican jay *Aphelocoma ultramarina* (Li, 1997); acorn woodpecker *Melanerpes formicivorus* (Haydock *et al*., 2001); Seychelles warbler *Acrocephalus sechellensis* (Richardson *et al*., 2001); brown jay *Cyanocorax morio* (Williams, 2004); white-throated magpie-jay *Calcoitta formosa* (Berg, 2005). See also Ben Mocha *et al*. (2023).

Consequently, it is often unclear how many non-breeding helpers need to be present in social groups to classify a species as a cooperative breeder (i.e. at least one/most/all of the helpers). Moreover, it is unclear how much breeding by helpers is allowed while still considering them as non-breeders (i.e. helpers may breed in <*X*% of litters/ broods or never breed). For instance, Lukas & Clutton-Brock (2012*a*, p. 2151) classified mammal species as cooperative breeders if 'a proportion of females do not breed regularly and show alloparental care'. In birds, Cornwallis *et al*. (2010, methods section) 'only classed species as cooperative if helpers did not breed or had zero-to-limited opportunities to breed'. The quantitative ambiguity of the terms 'proportion', 'regularly' or 'limited' leaves a wide scope for subjective interpretation that hampers an objective classification of species, comparison among studies and validation of species' classification by other researchers. Indeed, 22% of the 37 mammal species classified as cooperative breeders in Lukas & Clutton-Brock (2012*a*) or Lukas & Clutton-Brock (2017) were classified as non-cooperative breeders in the other one of these two studies (Tables 2 and S2). In birds, out of the 28 species classified by Cornwallis *et al*. (2010) as having helpers that 'did not breed or had zero-to-limited opportunities to breed' 21% were classified by Raihani & Clutton-Brock (2010) as species where subordinate females produce >10% of the group's reproductive output (Tables 2 and S3).

Our biological critique relies on the continuum of reproductive sharing among species with alloparental care (Sherman *et al*., 1995; Riehl, 2013; Ben Mocha *et al*., 2023). When correcting methodological biases [e.g. considering only groups with multiple sexually mature males or females (Spiering *et al*., 2010); or clutches in which shared parentage can occur (i.e. >1 offspring, Warrington *et al*., 2015)], extreme within-group reproductive skew is only found in 11 mammal and 12 bird species that were classified as cooperative breeders in data sets using a restrictive definition (Ben Mocha *et al*., 2023). Thus, if one uses a 'strict' version of the restrictive approach (i.e. helpers in groups of a cooperative breeding species must virtually never breed), only a few mammal and bird species can be qualified as cooperative breeders. On the contrary, if one uses a less rigid version of the restrictive approach (i.e. groups of cooperative breeding species must include 'some' helpers that 'do not always' breed), virtually all species with alloparental care will be classified as cooperative breeders. For instance, both banded mongooses (Mammalia: *Mungos mungo*) where 29% of adult female helpers do not breed during a breeding season (Cant, 2000) and dunnocks (Aves: *Prunella modularis*) where male helpers do not breed in 43% of the nests they attend (Burke *et al*., 1989) would be classified as cooperative breeders. Yet, these species were excluded as cooperative breeders in data sets that applied restrictive definitions (Cornwallis *et al*., 2010; Lukas & Clutton-Brock, 2012*a*).

We argue that the quantitative ambiguity embedded in restrictive definitions for cooperative breeding is not a contingent methodological shortcoming. Rather, this ambiguity is necessary to prevent restrictive definitions from *reductio ad absurdum* that will either make them exclusive to the point that too few species qualify as cooperative breeders (i.e. the strict version of the restrictive approach), or too inclusive until they are similar to the inclusive definitions (i.e. the less rigid version of the restrictive approach).

In sum, we propose to abandon definitions that restrict cooperative breeding to species with non-breeding helpers for two reasons. Methodologically, restrictive definitions rely on quantitatively ambiguous terms regarding 'non-breeding helpers'. They thereby hamper comparisons among studies and may induce cherry-picking of species within a data set. Biologically, if cooperative breeding is restricted to species with breeding monopolisation, only a fraction of species will qualify as cooperative breeders. We postulate that this small number of species is uninformative for understanding the evolution of cooperative breeding. Instead, we join the majority of scholars in supporting the inclusive approach to defining species as cooperative breeders regardless of the breeding status of helpers (e.g. Cockburn, 1998; Russell, 2004; for a comprehensive list see Table S1). Following previous studies (e.g. Sherman *et al.*, 1995; Riehl, 2013; Wang & Kimball, 2016), we suggest viewing within-group reproductive sharing among species with alloparental care as a continuum where species with extreme reproductive skew (e.g. some mole-rat species; Bishop *et al.*, 2004) represent one end, rather than a qualitatively different breeding system.

An important consequence of our suggestion is to abolish the categorial dichotomy between communal and cooperatively breeding species (e.g. Ligon & Burt, 2004; Clutton-Brock, 2006; Federico *et al.*, 2020). This is not to say that there are no quantitative differences in reproductive sharing across species with alloparental care, nor to discount the importance of these differences. Instead, we claim that the continuum of reproductive sharing among these species argues against an arbitrary cut-off to categorise species with a relatively low reproductive skew as non-cooperatively breeding.

III. INCONSISTENCY PROBLEM II: WHAT TYPE, EXTENT AND PREVALENCE OF ALLOPARENTAL CARE ARE SUFFICIENT TO QUALIFY SPECIES AS COOPERATIVE BREEDERS?

Alloparental care greatly varies within and among species. Within species, populations differ in the prevalence of breeding units that are assisted by helpers (see Fig. 2, Table S4, and Cockburn, 2020). Among species, the extent and type of alloparental care varies significantly (Isler & van Schaik, 2012). For example, Arabian babblers (*Turdoides squamiceps*) systematically and proactively feed (Carlisle & Zahavi, 1986; Ostreiher, 1997), preen (Dattner, 2005) and lead offspring between shelters (Ben Mocha, Mundry & Pika, 2019). By contrast, African elephants (*Loxodonta africana*) occasionally help with the locomotion and protection of others' offspring and only after calves express distress (Lee, 1987). Some scholars consider indirect care, such as territory defence, as alloparental care (e.g. Martín-Vivaldi *et al.*, 2002; Hughes *et al.*, 2003). Jennions & Macdonald (1994, p. 89) thus pointed out that without minimum criteria for alloparental care, 'by definition, all animals which are social during the breeding season are cooperative breeders' (see also Kimball, Parker & Bednarz, 2003; Shen *et al.*, 2017). This raises the question of which behaviours alloparents need to express to categorise the species as a cooperative breeder.

Below, we demonstrate that a lack of qualitative and quantitative criteria for alloparental care leads to substantial inconsistencies in the classification of species across data sets. We compared Isler & van Schaik's (2012) data set on the type and extent of alloparental care in mammals with Lukas & Clutton-Brock's (2012*a*) data set that classified mammal species as communal/cooperative breeders *versus* species that are not cooperative/communal breeders. We found only a moderate agreement [Cohen's kappa = 0.415 (possible range of kappa values is 0 1) (Landis & Koch, 1977)] between the species recorded by Isler & van Schaik (2012) as having >5% of nursing and/or carrying and/or proactive feeding provided by alloparents and the species classified by Lukas & Clutton-Brock (2012*a*) as cooperative/communal breeders (Tables 3 and S5). Furthermore, in the absence of the alloparental criteria used to classify species as cooperative breeders, verification and improvement of published data sets is not feasible. It is therefore not possible to understand why species recorded by Isler & van Schaik (2012) as exhibiting nursing and/or carrying and/or proactive feeding by alloparents were not classified by Lukas & Clutton-Brock (2012*a*) as cooperative nor communal breeders (e.g. *Saguinus geoffroyi*, *Cuon alpinus*, *Cynictis penicillata*, *Peromyscus maniculatus*, *Galea musteloides*, *Saimiri sciureus*).

Thus, defining the type, extent and prevalence of alloparental care to be used to classify species as cooperative breeding is crucial to increase comparability among studies. Below, we discuss these issues and suggest methodological solutions to reduce false-positive and false-negative classifications of species as cooperative breeders.

(1) Type of alloparental care behaviours

We propose considering as alloparental care every behaviour that is altered to benefit another group member's dependent offspring. This definition includes behaviours that occur before fertilisation [e.g. nest construction (Emlen, 1990; Stacey & Koenig, 1990)], before birth/hatching of another's offspring [e.g. feeding the pregnant/incubating female (Woodroffe & Vincent, 1994)] or during their postpartum development [e.g. proactive feeding of offspring (Ostreiher, 1997)]. Taking such an inclusive approach is important since distantly related species are likely to have diverse biological requirements for raising offspring. For example, infants in species that feed on non-transferable food (e.g. herbivores, baleen whales) often do not require prominent examples of alloparental care as allofeeding, but may receive help in locomotion (Lee, 1987) and babysitting (Whitehead, 1996). It is therefore important to examine the presence of alloparental care out of the set of parental care behaviours exhibited by the species in question.

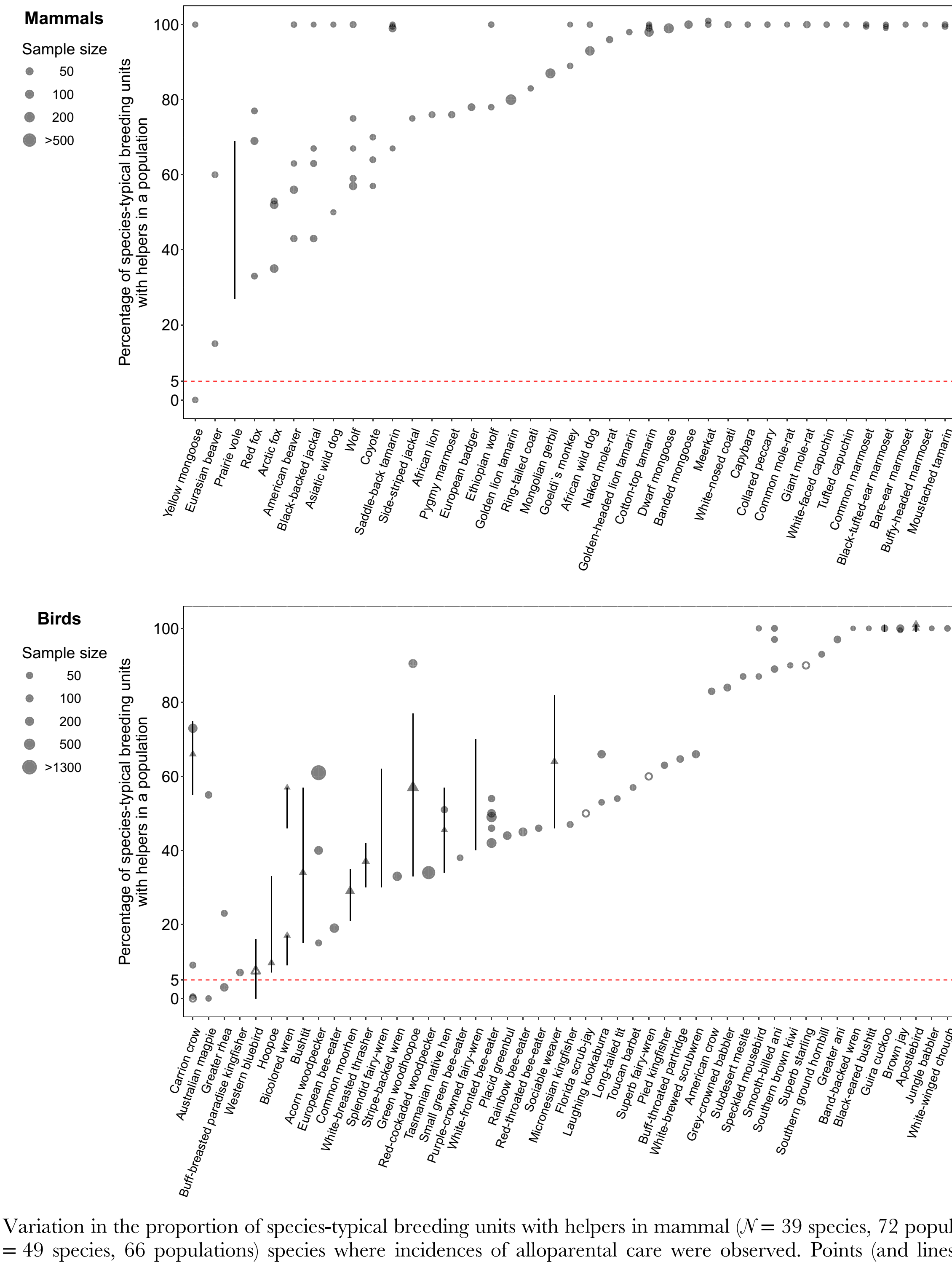

Fig. 2. Variation in the proportion of species-typical breeding units with helpers in mammal ($N = 39$ species, 72 populations) and bird ($N = 49$ species, 66 populations) species where incidences of alloparental care were observed. Points (and lines) represent percentages (and range over several years) of species-typical breeding units with helpers in specific populations [a breeding unit is defined as a social unit consisting of the species-typical provider/s of parental care (i.e. uniparental or biparental care), for instance, a male in the greater rhea *Rhea americana* or male and female in the jungle babbler *Turdoides striatus*]. For species without detailed data on group composition, groups with >2 non-infant animals of different sexes were regarded as having potential helpers. Triangles within lines represent the percentage and range of the same population. Symbol size indicates the sample size (empty symbols are data points without a sample size available). The red horizontal lines represent the 5% minimum threshold suggested in this study for considering a species as a cooperative breeder. For clarity, overlapping percentages were increased by 1 2%. See Table S4 for details and references.

Table 3. Agreement between two data sets examining alloparental care in 354 mammal species [87.9% agreement, Cohen's kappa = 0.415 (Cohen's kappa scores the degree of agreement after controlling for agreements that are expected by chance, the range of possible kappa values is 0 1), see Table S5 for data set]. Disagreements/agreements are marked in red/green respectively.

		Number of species Isler & van Schaik (2012) recorded as exhibiting (= yes) or not exhibiting (= no) >5% of nursing and/or carrying and/or proactive feeding by alloparents (see also Fig. 4)	
		Yes	No
Number of species classified as cooperative/communal breeders (= yes) or as exhibiting no alloparental care (= no) by Lukas & Clutton-Brock (2012*a*)	Yes	20	15
	No	28	291

(2) Reducing false-positive classification of species as cooperative breeders

Using this inclusive definition of alloparental care comes with the challenge of reducing false positives when classifying species as cooperative breeders or not. To this end, we propose three methodological reservations.

(*a*) *Type of alloparental care*

Our first reservation is to disregard by-product alloparental care. We define by-product alloparental care as behaviours that are maintained in the same way regardless of the presence of others' offspring, but still benefit these offspring. For instance, territorial defence, alarm calling and den cleaning occur in many social species even outside of the breeding season and may benefit others' offspring as a by-product of group living (Jennions & Macdonald, 1994; Hayes, 2000). Thus, the key criterion to confirm a certain behaviour as alloparental care is whether it is adjusted to accommodate the needs of others' offspring or the reproductive needs of their parents (Woodroffe & Vincent, 1994; Bshary & Bergmüller, 2008). Whether alloparental care is accommodated to the needs of others' offspring can be tested in different ways (e.g. Bustnes, 1993; Whitehead, 1996), including using hallmarks of intentionality (for an operational framework, see Ben Mocha & Burkart, 2021).

While the designated recipient of helping is easily inferred in behaviours that are directed toward a specific recipient (e.g. feeding; Blumstein & Armitage, 1999), the designated recipient of a helping behaviour with several

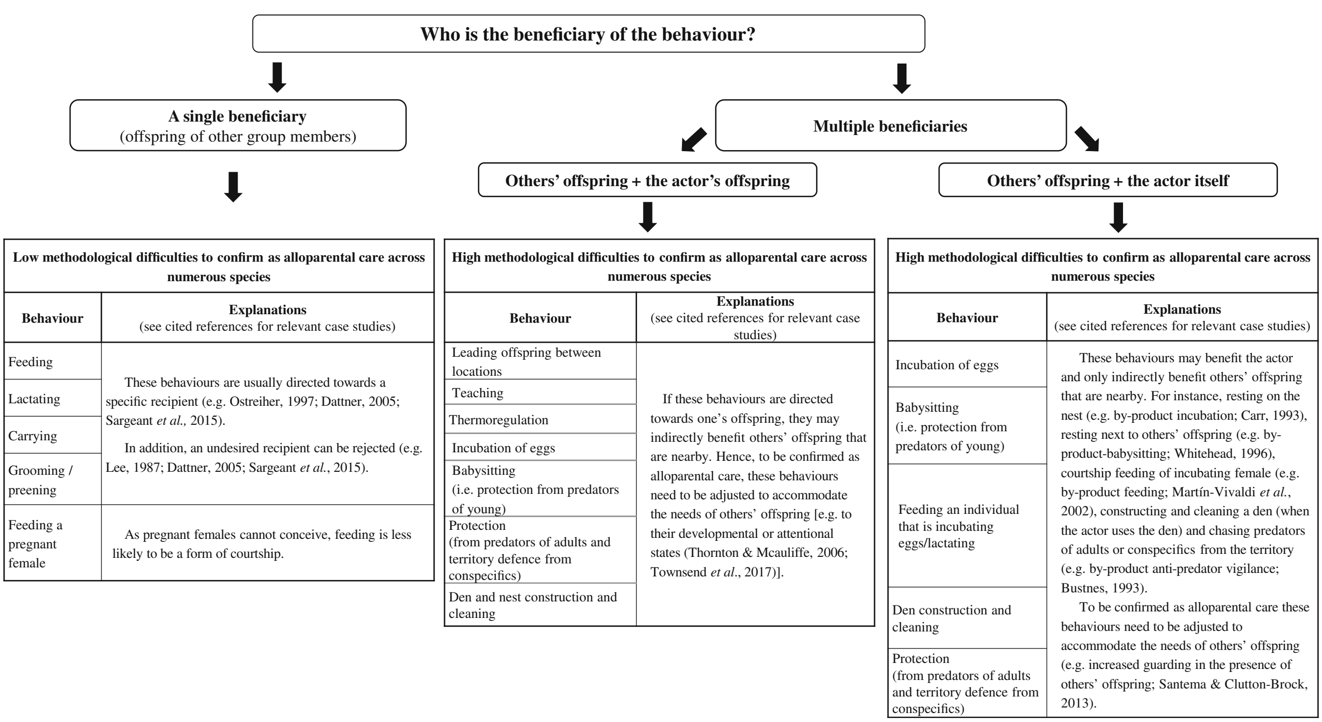

Fig. 3. Behaviours that may benefit others' offspring, categorised according to the methodological difficulties of confirming, across many species, whether they are aimed at helping others' offspring or whether they are by-product alloparental care.

beneficiaries (e.g. babysitting the babysitter's and others' offspring) is challenging. Consequently, helping behaviours for which it is methodologically difficult to determine whether they are true or by-product alloparental care are more likely to result in the misclassification of species as cooperative breeders. To facilitate the exclusion of by-product alloparental care, we listed helping behaviours according to the difficulty of confirming them as alloparental care across numerous species (Fig. 3). We propose that curators of data sets classify species using feeding, lactating, carrying, grooming/preening and feeding of a pregnant female. These behaviours have a low methodological difficulty to confirm them as alloparental care across species (Fig. 3). To avoid false-positive classification, we advise considering ambiguous behaviours (i.e. behaviours with high methodological difficulty in Fig. 3) as alloparental care only when solid evidence is available.

(*b*) *Minimum extent and prevalence of alloparental care*

Our second reservation is to reduce the risk of false-positive classifications of species as cooperative breeders, by carefully classifying species with limited prevalence (i.e. the proportion of breeding units with helpers out of the total number of breeding units in a population) or limited extent of alloparental care (i.e. alloparents provide a low proportion of care out of the total care provided to offspring in groups with helpers) (see also Griesser & Suzuki, 2016).

Limited prevalence and/or extent of alloparental care may be observed because it occurs in a non-systematic manner, for instance, non-systematic misdirected care by parents who lost their brood [compare non-systematic misdirected care in Price, Millington & Grant (1983) and Skutch (1987) with systematic care of failed breeders who then help other breeding pairs in western bluebirds *Sialia mexicana* (Dickinson, Koenig & Pitelka, 1996) and long-tailed tits *Aegithalos caudatus* (Hatchwell *et al.*, 2002)]. In well-studied species, even a rare behaviour such as misdirected care is likely to be documented, yet it should be expected to occur in only a small fraction of the breeding units (e.g. <5%; Griesser & Suzuki, 2016). However, if a few observations of alloparental care are sufficient to classify a species as a cooperative breeder, species will systematically be incorrectly classified as cooperative breeders as research effort increases. For example, Eurasian coots *Fulica atra* (Carr, 1993; Catley, 2011) and mute swans *Cygnus olor* (Włodarczyk & Kołaciński, 2001) are two widespread species that are often classified as cooperative breeders (e.g. Cockburn, 2006; Kenny, Birkhead & Green, 2017) based on a single observation of presumed helping. Indeed, such systematic false-positive classification may explain Griesser & Suzuki's (2016) finding that 'occasional' cooperative breeding is more common in well-studied species. See Griesser & Suzuki (2016) for a list of 152 occasional cooperative breeding bird species and Fig. 2 for data on the prevalence of breeding units with helpers in 138 populations of 88 mammal and bird species.

On the contrary, some well-studied species may exhibit limited, but systematic, prevalence and/or extent of alloparental care. This is, for example, the case in species living under eco-social conditions that only rarely favour cooperative breeding [e.g. western bluebird (Dickinson *et al.*, 1996); yellow mongoose *Cynictis penicillata* (Vidya *et al.*, 2009)] or chimpanzees (*Pan troglodytes*) where <4% of offspring carrying is performed by alloparents in different populations (Nishida, 1983; Pusey, 1990; Bădescu *et al.*, 2016). We propose considering these species with limited, yet systematic, alloparental care as expressing a limited capacity for alloparental care. While these species may present important opportunities to study the transition to cooperative breeding (Griesser *et al.*, 2017), we suggest excluding them from binary data sets as they do not represent clear examples of either of these groups (Griesser & Suzuki, 2016).

In sum, we propose that species where the average prevalence and/or extent of alloparental care is 1 5% should be classified with caution (Heldstab *et al.*, 2019). Specifically, well-studied species where 1 5% of breeding units in a population include alloparents but lack systematic helping should be classified as non-cooperative breeders. However, well-studied species should be excluded from binary data sets if they exhibit: (*i*) a systematically limited extent of alloparental care (i.e. in groups with alloparents, offspring receive an average of 1 5% care by alloparents), or (*ii*) a limited but systematic prevalence of alloparental care [i.e. an across-year average of 1 5% of breeding units with alloparents in at least one population. In species with re-directed helping (e.g. long-tailed tits; Hatchwell *et al.*, 2001), the percentage of breeding units with alloparents should be calculated from the number of breeding units at the breeding stage in which failed breeders usually join other breeding units].

Setting a minimum threshold for the prevalence and extent of alloparental care is a compromise between the need to avoid false-positive classifications of species as cooperative breeders (e.g. due to non-adaptive misdirected alloparental care) *versus* the need to avoid false-negative classifications of species as non-cooperative breeders. The ideal threshold should therefore be high enough to avoid as many false-positive classifications as possible while being low enough to exclude as few as possible cooperative breeding species with systematically limited alloparental care. We postulate that a 5% threshold represents a good balance between these contradicting needs based on the empirical cross-species distribution of prevalence of breeding units with alloparents (Fig. 2) and because, at least in mammals, it distinguishes between most species with and without alloparental care [see Heldstab *et al.* (2019), Fig. 4 and Table S6]. Nonetheless, further systematic research is needed to establish a well-justified threshold.

(*c*) *Species with limited data*

Inferring alloparental care requires substantial data from wild populations (Li & Brown, 2002; Roldán *et al.*, 2013). Yet to gain statistical power, curators often include all species with at least some behavioural data and classify species as non-cooperative breeders unless there is some evidence for alloparental care (Roldán *et al.*, 2013; Schradin, 2017). This

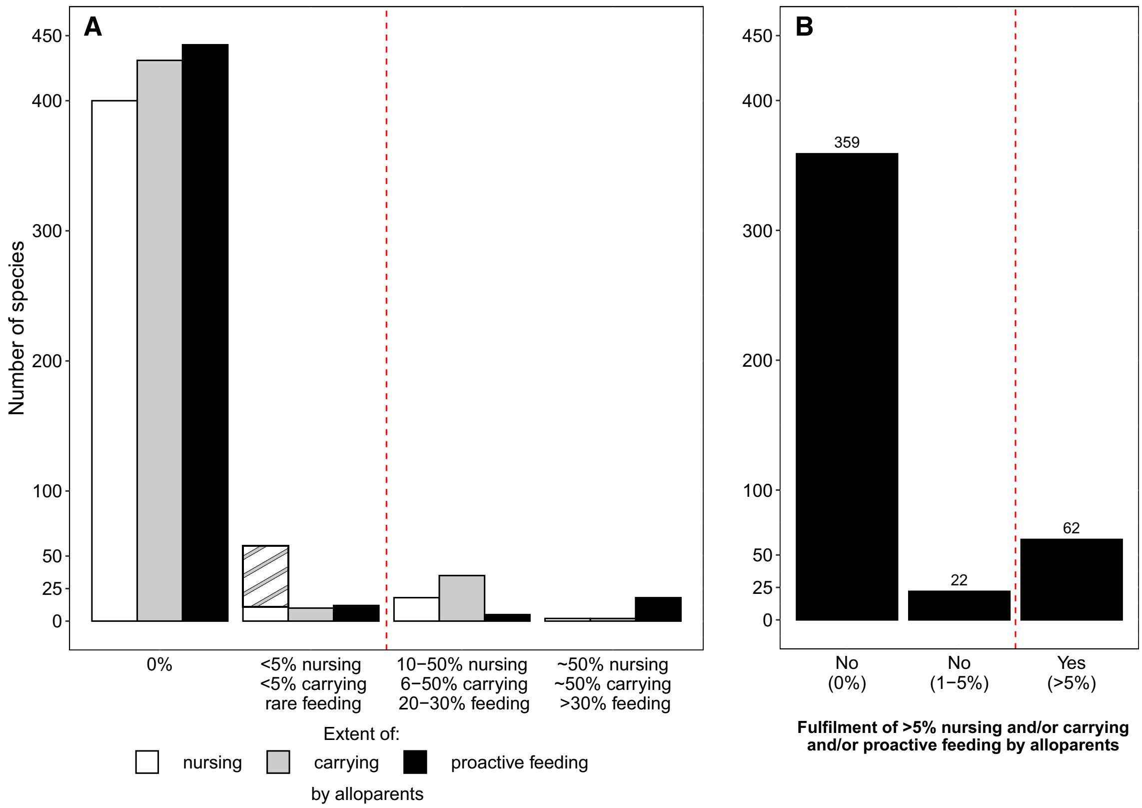

Fig. 4. The extent of nursing, carrying and proactive feeding performed by alloparents in mammal species [analysis of Isler & van Schaik's (2012) data set with the addition of 33 species from Heldstab *et al.* (2017)]. (A) Number of species exhibiting different extents of offspring nursing, carrying and proactive feeding by alloparents ($N = 478$ species). The striped rectangle represents 47 species where alloparents provide <10% of all nursing, but it is unclear whether the percentage is below or above 5% (35 of these 47 species were excluded from B, while 12 of these 47 species were included in B as they exhibited >5% of carrying and/or allofeeding). (B) Number of mammal species where >5% of nursing and/or carrying and/or proactive feeding of offspring is provided by alloparents ($N = 443$ species; see Table S6 for a list of species with alloparental care).

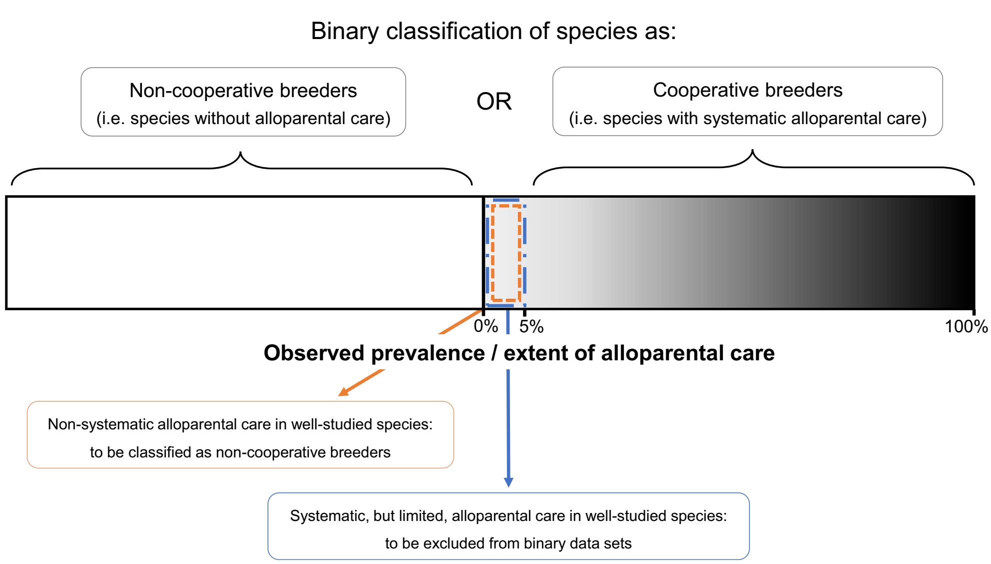

Fig. 5. Biological rationales for binary classification of species as cooperative *versus* non-cooperative breeders. The *x*-axis represents the extent of proactive alloparental care across species and/or the prevalence of breeding units with helpers across species.

classification default results in species with limited data being more likely to be incorrectly classified as non-cooperative breeders. This is especially true for taxa where most natural activity is not easily observed; for instance, birds in tropical rain forests, marine mammals (e.g. Whitehead, 1996) and bats (Heldstab *et al.*, 2019). We therefore urge curators either to indicate species whose classification is based on limited data (Cockburn, 2006; Ben Mocha *et al.*, 2023) or to exclude them from comparative studies until further data become available (Griesser & Suzuki, 2016; Schradin, 2017).

IV. ADVANCING COMPARATIVE RESEARCH WITH A UNIFIED DEFINITION

In this section, we present an operational definition for the binary classification of species as cooperative or non-cooperative breeders. Alloparental care is the core element of all definitions of cooperative breeding (Table 1) and constitutes the primary interest in this breeding system (e.g. Skutch, 1935; Wang & Kimball, 2016). Our principle approach is thus to consider cooperative breeding as synonymous with alloparental care. Accordingly, we propose to consider all species that exhibit systematic and proactive alloparental care as cooperative breeders (see also Jennions & Macdonald, 1994; Sherman *et al.*, 1995; Cockburn, 2003; Fig. 5). We propose the following operational definition: cooperative breeding is a reproductive system where >5% of broods/litters in at least one population receive species-typical parental care (i.e. maternal, paternal or bi-parental care) and conspecifics provide proactive alloparental care that fulfils >5% of at least one type of the offspring's needs. Below, we discuss the biological rationales that underlie the key elements of this definition.

(1) Species-typical parental care and conspecific alloparents

By requiring species-typical parental care, our definition excludes cases of intra-specific parasitism and extra-pair parentage. The requirement of species-typical parental care also enables the inclusion of species with uniparental care as cooperative breeders, which are excluded by definitions that require care by more than two individuals (see Tables 1 and S1). For example, in greater rheas (*Rhea americana*), associations of two or more fathers provide paternal and alloparental care while mothers usually do not provide parental care (Codenotti & Alvarez, 1997; see also Vehrencamp, 2000).

In addition, our definition requires alloparents to be conspecifics to exclude from cooperative breeding cases of inter-specific parasitism (e.g. cuckoos) and inter-specific misdirected alloparental care (Griesser & Suzuki, 2016).

(2) Alloparental care criteria

Our definition specifies qualitative criteria of alloparental care, as well as quantitative minimum thresholds for the prevalence and extent of alloparental care (see Section III). As our definition only specifies minimum thresholds for alloparental care, it is designed to capture species with a capacity for systematic alloparental care regardless of its level of expression. Nonetheless, both the prevalence and extent of alloparental care vary quantitatively within and among species (e.g. Isler & van Schaik, 2012; Heldstab *et al.*, 2019; Fig. 2). The binary classification of species as cooperative *versus* non-cooperative does not capture this potentially important quantitative variations in the expression of alloparental care. However, the level of alloparental care may critically affect social cognition (Burkart & van Schaik, 2010; Burkart *et al.*, 2014), teaching (Hoppitt *et al.*, 2008) or brain size (Heldstab *et al.*, 2019; Griesser *et al.*, 2023). If this is the case, contrasting non-cooperative breeding with cooperative breeding species with a low extent of alloparental care may not have sufficient power to detect differences. To avoid this potential problem, we recommend that comparative studies control statistically for the prevalence and extent of alloparental care across species (Burkart & van Schaik, 2010; Burkart *et al.*, 2014). Recently developed statistical methods using STAN (Carpenter *et al.*, 2017) can model intra-population variation of traits and thereby may allow assessment of how variation in the prevalence and extent of alloparental care affects other traits (e.g. Olivier *et al.*, 2022).

(3) Sub-categories of cooperative breeding

Our definition of cooperative breeding encompasses all species with systematic and proactive alloparental care. Nevertheless, cooperative breeding may be realised to different extents (Figs 2–4) and in diverse forms within and across species (e.g. alloparents may be kin or non-kin, groups may be family units, multi-level societies or other types of social systems). Different forms of cooperative breeding likely evolved due to different selective pressures (Riehl, 2013; Griesser *et al.*, 2017; Shen *et al.*, 2017). We make two comments regarding the relationship between our unified definition and the diversity of cooperative breeding groups. First, even if a specific sub-category of cooperative breeding is the focus of a study (e.g. species in which alloparental care is provided by allegedly non-reproductive helpers), it is important not to classify species from other sub-categories of cooperative breeding as non-cooperative breeding species. Namely, we recommend not creating a binary data set in which a specific sub-category of cooperative breeding species is compared against a cluster of species with and without alloparental care (e.g. Cornwallis *et al.*, 2010; Lukas & Clutton-Brock, 2012*a*).

Second, cooperative breeding is often not realised in a homogeneous form and different forms of cooperative breeding co-occur within the same population and species. For example, within the same population of Seychelles warblers (*Acrocephalus sechellensis*), 71% of breeding units consist of socially monogamous pairs and 29% of breeding units are groups with breeders and helpers (Richardson, Burke & Komdeur, 2002). In groups with multiple females, 40% of groups include a single breeding female while 60% of groups include multiple breeding females (Richardson *et al.*, 2001).

Thus, the classification of Seychelles warblers as either a monogamous or plural breeder species would be an oversimplification. Classification of cooperative breeding species into sub-categories should take into consideration this within-species quantitative variability. Further conceptual and empirical research about how exactly to conduct such non-dichotomous classification of sub-categories of cooperative breeding species is required.

(4) Beyond binary classification

This review discusses the binary classification of species as cooperative *versus* non-cooperative breeders. However, these two categories include diverse species that do not represent biologically homogeneous groups in other aspects besides engagement in alloparental care. As a result, when the response variable is classified in a binary manner, contrasting patterns exhibited by sub-categories of species clustered together may statistically obscure each other's effect (Griesser *et al*., 2017; Shen *et al*., 2017). For example, analyses may benefit from dividing the group of cooperative breeding species into sub-groups according to whether alloparental care evolved due to 'resource defence' or 'collective action' benefits (see Shen *et al*., 2017). On the other hand, the cooperative and non-cooperative breeding groups of species may be subdivided into non-family-living and family-living species (Drobniak *et al*., 2015; Griesser *et al*., 2017). We thereby highlight the limitations of using a binary classification of species as a response variable, and call for further use of multinomial classifications of species in statistical analyses.

V. CONCLUSIONS

(1) Inconsistent definitions of cooperative breeding hamper valid comparisons among data sets and analyses (Sherman *et al*., 1995; Pruett-Jones, 2004). More consistent use of definitions is fundamental to progress in this field, thereby ensuring that different studies of cooperative breeding indeed examine the same phenomenon and group of species (Fig. 1).

(2) Equally important for comparative and replicable research is setting distinct and transparent quantitative and qualitative criteria for the alloparental care required to classify species as cooperative breeders (Schradin, 2017; Ben Mocha *et al*., 2023).

(3) Rigorous data regarding the presence, type and extent of alloparental care is currently limited for most species (Riehl, 2013; Roldán *et al*., 2013; Heldstab, van Schaik & Isler, 2017). In the absence of sufficient data on alloparental care, we urge curators to exclude these species from data sets to ensure scientific accuracy until more data are gathered. We thereby join other researchers of cooperative breeding (e.g. Griesser & Suzuki, 2016; Heldstab *et al*., 2017; Schradin, 2017) and statisticians (e.g. Meng, 2018; Bradley *et al*., 2021) in prioritising a modest sample size of reliably classified species over a more comprehensive sample with a higher probability of false classifications of breeding systems. To facilitate comparative research on alloparental care, we provide data sets on the prevalence (Table S4) and extent (Table S6) of alloparental care in mammals and birds.

(4) Our principal proposal is to consider cooperative breeding as synonymous with species that demonstrate systematic and proactive alloparental care. As alloparental care is exhibited in manifold forms and extents (Figs 2 4), we join previous authors who suggest considering cooperative breeding as an umbrella term for various forms of reliance on alloparental care (Sherman *et al*., 1995; Burkart, van Schaik & Griesser, 2017; Shen *et al*., 2017; Lin *et al*., 2019).

(5) Humans engage in systematic and proactive alloparental care (Hewlett, 1993; Lahdenperä *et al*., 2004; Hrdy, 2007; Hill & Hurtado, 2009). Our definition therefore classifies humans as a cooperative breeding species (see also Burkart *et al*., 2009). We thereby highlight the importance of comparative research on cooperative breeding for evolutionary anthropology (Burkart *et al*., 2017; Tomasello & Gonzales-Cabrera, 2017).

(6) While this work focuses on mammals and birds, cooperative breeding is also found in fishes (Taborsky, 2016) and, according to some definitions, in invertebrates [see discussion in Sherman *et al*. (1995); but also Rubenstein, Botero & Lacey (2016)]. Empirical and conceptual studies that extend the applicability of the presented framework to other taxa would further benefit a more comprehensive view of the phenomenon of cooperative breeding.

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VIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Definitions for cooperative breeding used in comparative and theoretical studies in ornithology, mammalogy and evolutionary anthropology since 1974.

Table S2. Comparison between Lukas & Clutton-Brock (2012*a*) and Lukas & Clutton-Brock (2017) lists of cooperative breeding mammals.

Table S3. Comparison between Cornwallis *et al.* (2010) and Raihani & Clutton-Brock (2010) lists of cooperative breeding bird species that exhibit extreme reproductive skew [only species classified by Cornwallis *et al.* (2010) as cooperative breeders were compared].

Table S4. Prevalence of species-typical breeding units with at least one alloparent in wild populations of bird and mammal species that were reported to exhibit alloparental care.

Table S5. Comparison between Isler & van Schaik (2012) and Lukas & Clutton-Brock (2012*a*) data sets regarding the presence of alloparental care in mammal species.

Table S6. Mammal species listed according to the extent of nursing, carrying and allofeeding by alloparents [summary of data from Isler & van Schaik (2012) and Heldstab *et al.* (2017)].

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