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1 **The causes and consequences of inbreeding avoidance and**
2 **tolerance in cooperatively breeding vertebrates**

3 Hazel J Nichols

4 School of Natural Sciences and Psychology, Liverpool John Moores University, Byrom Street

5 Liverpool, L3 3AF

6 h.j.nichols@ljmu.ac.uk

7 **Short title:** Inbreeding in cooperative breeders

8 **Abstract**

9 Cooperative breeders provide a particularly interesting scenario for studying inbreeding.
10 Such populations are viscous due to delayed dispersal and short dispersal distances, resulting in the
11 build-up of relatives in the local population. This leads to a high risk of inbreeding, and consequently
12 of inbreeding depression. This has driven the evolution of an array of inbreeding avoidance
13 mechanisms resulting in a relatively low level of close inbreeding in the majority of cooperative
14 breeders. However, there are a number of species where inbreeding occurs relatively frequently.
15 The presence of regular inbreeding (in cases where inbreeding is not a result of recent population
16 declines), suggests that inbreeding tolerance and even preference can evolve under some
17 circumstances. Both inbreeding and inbreeding avoidance mechanisms have enormous downstream
18 fitness consequences for cooperative breeding species. For example, they can influence
19 reproductive dynamics leading to a monopolisation of breeding opportunities by dominant
20 individuals. Inbreeding and its avoidance are also likely to impact on the evolution of cooperative
21 breeding itself through influencing levels of relatedness between potential cooperators. Finally, in
22 some cooperative breeders, a high degree of inbreeding avoidance can be detrimental to population
23 viability, and hence is of particular concern to conservationists. In this review, I discuss these issues
24 in detail and also briefly consider recent advances in the methods available for the study of
25 inbreeding in natural populations.

26 **Key words:** cooperation, inbreeding, incest, heterozygosity, kin-recognition, relatedness, dispersal,
27 extra-pair paternity

28 **Introduction**

29 Breeding between close relatives (Box 1) generally entails a fitness cost, known as
30 inbreeding depression (Darwin 1900), and mainly results from the increased homozygosity of
31 recessive deleterious alleles. The detrimental effects of inbreeding are well documented empirically

32 under laboratory and captive conditions as well as in the wild (Keller & Waller 2002), and can lead to
33 a substantial reduction in offspring fitness (Charlesworth & Charlesworth 1987, Ralls, Ballou &
34 Templeton 1988). It is consequently not surprising that inbreeding avoidance is widespread in the
35 animal kingdom (Keller & Waller 2002). However, inbreeding avoidance is also associated with costs.
36 Dispersal to find an unrelated mate is commonly associated with increased mortality (Clutton-Brock
37 & Lukas 2012) whereas ‘too much’ outbreeding can reduce offspring fitness by breaking up adaptive
38 gene clusters (known as outbreeding depression (Bateson 1983, Helgason *et al.* 2008)). Furthermore,
39 theoretical work predicts that inbreeding can have a substantial positive effect on inclusive fitness
40 through increasing the reproductive success of relatives (Dawkins 1979, Lehmann & Perrin 2003,
41 Kokko & Ots 2006) and increasing the benefits of cooperation (Hamilton 1964), implying that even
42 close inbreeding should be tolerated under some circumstances (Kokko & Ots 2006, Thunken *et al.*
43 2007).

44 How these conflicting selection pressures are resolved has long been recognised as a
45 dilemma (reviewed in Szulkin *et al.* (2013)), but the natural history of inbreeding has proved
46 particularly difficult to study. Empirical work on wild populations has often been hampered by the
47 difficulty of obtaining accurate coefficients of inbreeding (Pemberton 2004), and many short-term
48 studies may fail to detect environment-dependent inbreeding depression. Furthermore, studies on
49 populations that have suffered recent declines or habitat fragmentation may lack relevance due to
50 artificially high levels of inbreeding (Jamieson *et al.* 2009). On the other hand, laboratory
51 investigations can fail to replicate natural social or environmental conditions (Pemberton 2008),
52 while theoretical predictions often appear to mismatch empirical evidence (Lehmann & Perrin 2003,
53 Kokko & Ots 2006). Moreover, few attempts have been made to study the interplay between
54 inbreeding and cooperative behaviour. At its most basic level, inbreeding and inbreeding avoidance
55 both affect patterns of relatedness, which can in turn affect the evolution of cooperation (Koenig &
56 Haydock 2004). In addition, the ‘quality’ of individuals can influence reproductive competition and
57 cooperative behaviours (Heinsohn & Legge 1999, Meagher, Penn & Potts 2000), and this may also be

58 influenced by inbreeding (Meagher et al. 2000). Consequently, studies of inbreeding in highly
59 cooperative species are well-placed to provide insights into its effects on the dynamics and evolution
60 of animal social systems.

61 Despite the logistical challenges, substantial advances have been made in the field of
62 inbreeding in cooperative breeders since the last major review of Koenig and Haydock (2004). First,
63 although data on many species is still lacking, the growing number of long-term studies of wild
64 populations of cooperative breeders incorporating genetic, behavioural, life-history and
65 environmental data have allowed us to quantify the occurrence and distribution of inbreeding in
66 many more species than previously possible (Koenig & Dickinson 2016). Such studies have also
67 allowed us to investigate the diversity of ways by which inbreeding is avoided, and also to uncover
68 some of the impacts of inbreeding avoidance on individual fitness, dispersal patterns, group
69 structure and relatedness dynamics. Furthermore, methods for studying inbreeding have improved
70 substantially over recent years (Pemberton 2008, Hoffman et al. 2014, Bérénos et al. 2016, Huisman
71 et al. 2016). In particular there have been consistent advances in the genetic methods available to
72 identify inbreeding, and also in our understanding of the caveats of these methods (Pemberton 2008,
73 Szulkin et al. 2010). Such methods therefore provide much promise for expanding our knowledge of
74 the natural history of inbreeding in the wild.

75 In this review, I first highlight why inbreeding and inbreeding avoidance are of particular
76 interest in cooperatively breeding species. I then go on to evaluate the prevalence and distribution
77 of inbreeding among cooperative species, before exploring ways through which inbreeding is
78 avoided, and why some species may tolerate frequent inbreeding. Following this, I discuss the
79 consequences of inbreeding avoidance and tolerance for cooperative breeders. Finally, I outline
80 developments in the methods used to study inbreeding and briefly discuss their relative merits.

Box 1: Definitions

Inbreeding: mating between individuals with one or more common ancestors.

Close inbreeding: mating between first order relatives such as full-siblings or parent and offspring, often referred to as incest. Offspring resulting from close inbreeding have an inbreeding coefficient (f) of 0.25.

Moderate inbreeding: Mating between second order relatives such as half-siblings, uncle and niece, aunt and nephew, grandparent and grandchild or double first cousins. Here, f of offspring is 0.125.

Distant or weak inbreeding: Any inbreeding below the second-order relative level. Here, f is below 0.125, but above 0.

Cooperative breeder: here defined in its broadest sense as species where individuals other than parents care for offspring.

81

82 Why are cooperative breeders particularly interesting for the study of inbreeding?

83 Cooperative breeders present a particularly interesting scenario for studying inbreeding (for
84 definitions see Box 1). Here, dispersal is usually delayed until after sexual maturity, and offspring
85 remain with their parents and help to rear subsequent broods or litters, often consisting of full or
86 half-siblings (Koenig & Dickinson 2004, Russell 2004, Lukas & Clutton-Brock 2012). This leads to a
87 situation where groups often, although not always, consist of close opposite-sex relatives with the
88 potential to inbreed (Koenig & Haydock 2004). Early studies predicted that inbreeding would
89 enhance cooperation through increasing relatedness between group members (Hamilton 1964,
90 Marshall et al. 2002). This premise appeared to be confirmed by findings of a high level of band-
91 sharing in DNA fingerprints within eusocial naked mole-rat *Heterocephalus glaber* colonies,
92 demonstrating close inbreeding in one of the most cooperative vertebrate societies known (Reeve et

93 *al.* 1990). However, the level of inbreeding in naked mole-rats has since been re-evaluated.
94 Subsequent studies showed higher dispersal levels than previously thought (Braude 2000,
95 Pemberton 2008), evidence of inbreeding avoidance (Ciszek 2000) and inbreeding depression (Ross-
96 Gillespie, O’Riain & Keller 2007), and biases in the original sampling towards a severely bottlenecked
97 population (Ingram *et al.* 2015). In addition, studies of other cooperative breeders, including another
98 eusocial mole-rat *Fukomys damarensis*, have demonstrated that regular inbreeding is not required
99 for the evolution of extreme social complexity, cooperation and reproductive skew (Burland *et al.*
100 2002, Pemberton 2004).

101 Despite opportunities for regular inbreeding in cooperative breeders, close and moderate
102 levels of inbreeding have been shown to be rare within most cooperative species (Koenig & Haydock
103 2004). As a typical example, in the Florida scrub jay, a socially and genetically monogamous
104 cooperative breeder, only 0.6% of nestlings are the product of close inbreeding (Fitzpatrick &
105 Bowman 2016). A low level of inbreeding across cooperative breeders likely results from a lack of
106 breeding from subordinate helpers, in part due to individual restraint when there are no unrelated
107 group-members to breed with, and partly due to suppression by dominant breeders (O’Riain *et al.*
108 2000, Koenig & Dickinson 2004, Huisman *et al.* 2016).

109 Within-group inbreeding may be more likely to occur in species where mate-choice is
110 particularly constrained. For example, in the banded mongoose *Mungos mungo* (Figure 1), which
111 lives in large mixed-sex groups with relatively low reproductive skew, the majority of breeding
112 occurs within groups despite the presence of close relatives as potential mates (Nichols *et al.* 2014).
113 This is likely due to the high cost of seeking mates from outside the social group (Nichols, Cant &
114 Sanderson 2015) and leads to 9% of pups being the product of close inbreeding and 17% of pups
115 being the product of moderate inbreeding (Nichols *et al.* 2014) (see Box 1 for definitions). Several
116 other cooperatively breeding vertebrates have been proposed to inbreed regularly, including both
117 birds (pukekos *Porphyrio melanotus* (Craig & Jamieson 1988), green wood hoopoes *Phoeniculus*

118 *purpureus* (Du Plessis 1992), common moorhens *Gallinula chloropus* (McRae 1996) and Seychelles
119 warblers *Acrocephalus sechellensis* (Richardson, Komdeur & Burke 2004)) and mammals (such as
120 dwarf mongooses *Helogale parvula* (Keane, Creel & Waser 1996) and red wolves *Canis rufus*
121 (Sparkman *et al.* 2012)). However, genetic data is often either unavailable or is not of sufficient
122 quality to accurately quantify inbreeding rate (reviewed in Koenig & Haydock, 2004). Exceptions are
123 the Seychelles warbler and the red wolf, which have microsatellite genotypes available (see Box 2).
124 In the Seychelles warbler, 5% of pairings were likely to be between first order relatives, while in the
125 red wolf, 8% of pairs were close relatives. However, both of these species are endangered and have
126 experienced severe bottlenecks which may have both eroded genetic diversity and constrained mate
127 choice (Richardson *et al.* 2004, Sparkman *et al.* 2012), so neither may be representative of wild
128 animal populations.

129 The examples of the red wolf and Seychelles warbler highlight the need to interpret the
130 observed inbreeding strategy in the context of historical and current population ecology. In some
131 populations, the encounter rate with opposite sex relatives is a product of the species breeding
132 system and patterns of dispersal. However in others the encounter rate may have been largely
133 skewed by recent changes to population size and connectivity, which results in a higher frequency of
134 inbreeding (Szulkin *et al.* 2013). Indeed, it is only under stable, long-term environmental selective
135 pressures that behavioural mechanisms of inbreeding tolerance and/or avoidance could have
136 evolved.

137 The broadest trend in terms of the distribution of inbreeding within cooperative breeders is
138 that inbreeding appears more common at the population (between-group) level than at the within-
139 group level. For example, inbreeding may occur when an individual immigrates into a group already
140 containing kin with which the disperser is unfamiliar. In meerkats *Suricata suricatta* (Figure 1), which
141 live in large groups of close kin with the occasional unrelated immigrant, almost all inbreeding occurs
142 at the between-group level (Nielsen *et al.* 2012). Similarly, in two species of canids, within-group

143 inbreeding is avoided, but outside of the natal group, mates were selected independent of
144 relatedness (Geffen *et al.* 2011). Such patterns may occur because the costs of avoiding inbreeding
145 at the population level generally exceed the benefits; avoiding kin would require a sophisticated
146 method of inbreeding avoidance and could result in lost breeding opportunities (Brouwer *et al.*
147 2011). Also, in a large outbred population, there is unlikely to be strong selection to avoid
148 inbreeding at a population level; in Geffen *et al.*'s (2011) study, the probability of encountering full
149 siblings as potential mates outside of the natal group was as low as 1%, depending on the population.

150 **Why is inbreeding avoided?**

151 The primary cost of inbreeding is inbreeding depression, resulting mainly from an increase in
152 homozygosity which allows for the expression of harmful but recessive alleles (reviewed by
153 Charlesworth and Willis (2009)). Inbreeding depression has been found in the vast majority of
154 species where it has been investigated (reviewed by Pusey and Wolf (1996)) and can manifest in
155 many forms such as reduced growth (Brzeski *et al.* 2014), survival and reproductive success (Liberg
156 *et al.* 2005), and increased susceptibility to disease (Townsend *et al.* 2009). Although inbreeding
157 depression is most severe in pairings between first order relatives, it also occurs to some degree
158 between moderate and distant relatives. In cooperatively breeding meerkats, inbreeding depression
159 was found in a range of early life traits even though close inbreeding was successfully avoided in the
160 population (Nielsen *et al.* 2012). Furthermore, although inbreeding depression is usually most severe
161 in juveniles, the development of more powerful techniques for detecting inbreeding (**Box 2**) are also
162 resulting in inbreeding depression being found in adults. For example, in (non-cooperative) red deer
163 *Cervus elaphus*, matings between half-siblings resulted in a decline in lifetime breeding success in
164 females by 72% and males by 95% (Huisman *et al.* 2016). In addition, inbreeding depression can have
165 cross-generational effects, with inbred mothers producing smaller lambs in (non-cooperative) Soay
166 sheep *Ovis aries* (Bérénos *et al.* 2016) and fawns with lower survival to recruitment in red deer
167 (Huisman *et al.* 2016).

168 **How is inbreeding avoided?**

169 Despite living and breeding while surrounded by kin, cooperative breeders often avoid close
170 inbreeding. This is accomplished through a wide variety of methods, outlined below. These methods
171 are not mutually exclusive and there is often evidence for a single species avoiding kin as mates in a
172 variety of ways, depending upon the context.

173 ***Dispersal***

174 Although cooperative breeders typically show delayed dispersal, this does not mean that
175 dispersal is absent; helping is usually a temporary role, and can last for less than one breeding
176 season in some species (Sharp *et al.* 2005). When dispersal does occur, there is often evidence that it
177 is related to inbreeding avoidance. First, dispersal and/or greater dispersal distances are often
178 biased towards one sex, which reduces the encounter rate between opposite sex relatives. It is
179 therefore not surprising that inbreeding avoidance has been proposed as one of the main drivers of
180 dispersal behaviour (Clutton-Brock 1989, Szulkin & Sheldon 2008, Clutton-Brock & Lukas 2012).
181 Second, even when sex-biased dispersal doesn't occur, typical dispersal distances can put dispersers
182 out of the range within which close relatives are found (Cockburn *et al.* 2003, Nelson-Flower *et al.*
183 2012). Third, inbreeding avoidance may sometimes trigger dominant breeders to give up their
184 breeding position and disperse. For example, if a dominant breeder dies, the remaining dominant
185 may abandon their position if the highest-ranking opposite-sex subordinate is a close relative
186 (Cockburn *et al.* 2003). However, while inbreeding avoidance may play a part in determining
187 patterns of dispersal, cooperative breeders of either sex generally disperse only short distances
188 (Zack 1990, Riehl & Stern 2015), and in many species, inbreeding avoidance is not the primary
189 determinant of dispersal decisions. For example, in two species of cooperative mongoose, aggressive
190 eviction events occurring almost exclusively whilst dominant females are pregnant indicate that
191 reproductive competition, rather than inbreeding avoidance is the main driver of dispersal, at least
192 among females (Cant *et al.* 2010, Clutton-Brock *et al.* 2010).

193 One particular type of dispersal that has received limited attention is divorce. Divorce in
194 social monogamous species has been traditionally associated with low breeding success, or
195 movement to a breeding vacancy on a better quality territory (Ens, Safriel & Harris 1993). However,
196 in cooperative breeders, incest avoidance has also been implicated. Aranzamendi *et al.* (2016) found
197 that incest avoidance was the key predictor of divorce in the purple-crowned fairy-wren *Malurus*
198 *coronatus*, with 64% of incestuous partnerships divorcing shortly after formation, and none lasting
199 over 1 year. Similar patterns have been found in other cooperatively breeding birds, with females
200 that become socially paired with their sons after their partner dies often divorcing their sons but
201 accepting unrelated helpers as mates (Daniels & Walters 2000, Cockburn *et al.* 2003).

202 ***Kin recognition***

203 Among cooperative breeders, where populations are viscous and dispersal delayed,
204 selection pressure to evolve mechanisms of inbreeding avoidance other than dispersal is likely to be
205 particularly high (reviewed across birds by Riehl and Stern (2015)). Supporting this idea, a literature
206 search of mating patterns in birds found that almost all cooperative species with pedigree or genetic
207 data showed evidence of inbreeding avoidance via kin discrimination whilst very few singular-pair
208 species did (Jamieson *et al.* 2009). There are various ways by which kin-recognition may occur,
209 including learning to identify familiar relatives, using simple rules to identify likely kin, and assessing
210 genetic relatedness directly via phenotype matching (Komdeur & Hatchwell 1999). Note that
211 although these mechanisms are often treated as being mutually exclusive, many species may use a
212 combination of mechanisms that are context dependent.

213 The degree of association between individuals among group-living species usually co-varies
214 with kinship as social groups usually contain family members. It is therefore often possible for
215 individuals to assess the likely level of relatedness between themselves and other individuals by
216 associative learning through social familiarity (Moore & Ali 1984), a mechanism which appears to be
217 both effective and widespread (Pusey & Wolf 1996). Often there is a critical period in which the

218 learning of relatives takes place, usually during infancy (Kuester, Paul & Arnemann 1994), although
219 continued association with relatives through phenotypic changes is important for kin recognition in
220 some species (Ihle & Forstmeier 2013).

221 Among cooperative species, recognising relatives is also likely to be important in directing
222 kin-selected helping behaviour, hence many studies demonstrating evidence of kin recognition come
223 from investigations of helping decisions. Particularly revealing are experiments that have involved
224 manipulating the degree of relatedness between individuals, whilst keeping familiarity constant (and
225 vice versa). In Seychelles warblers and western bluebirds *Sialia mexicana*, cross-fostered offspring
226 from extra-pair matings help at their adoptive parents nest at similar rates to true offspring
227 (Komdeur, Richardson & Burke 2004, Dickinson *et al.* 2016). Here, individuals appear to use
228 familiarity to adults that tended to them prior to fledging as a proxy for relatedness despite
229 relatively high rates of extra pair paternity (Komdeur *et al.* 2004, Dickinson *et al.* 2016). Similarly, in
230 the long-tailed tit *Aegithalos caudatus*, Russell and Hatchwell (2001) conducted an experiment
231 where they provided potential helpers with a choice of nests to help at that either contained
232 relatives or non-relatives. In 94% of cases, helpers chose to help at the nests of relatives,
233 demonstrating kin recognition. Further experiments on the same study system showed that learned
234 vocal cues are used as a mechanism for kin-recognition in this species, with nestlings learning and
235 emulating the calls of their close family (Sharp *et al.* 2005). Indeed, learned vocal cues may provide a
236 reliable indication of relatedness across many bird species (reviewed by Riehl and Stern (2015),
237 McDonald and Wright (2011), Hatchwell (2016)).

238 Whilst familiarity is often a good indicator of relatedness, in some societies the use of
239 familiarity alone to identify potential relatives may not be sufficient to avoid inbreeding, for example
240 in species with a high level of extra-group paternity (EGP) or where multiple females contribute to a
241 communal litter or brood. Here, individuals may follow behavioural rules, some of which rely on
242 familiarity and some of which do not. One simple cue to relatedness in relatively viscous populations

243 is likely to be distance. In red-winged fairywrens *Malurus elegans*, females that have inherited a
244 territory are more likely to seek EGP, or seek EGP from further away than females that have
245 dispersed before breeding (Brouwer et al. 2011). Similarly, superb fairy-wren *Malurus cyaneus*, and
246 pied babbler *Turdoides bicolor* females disperse further from their natal groups than non-natal
247 groups (Cockburn et al. 2003, Nelson-Flower et al. 2012). Other potential rules may include
248 discriminating against particular age groups likely to contain relatives, or based on previous mating
249 experience, for example to avoid daughters of females that males previously mated with (Archie et
250 al. 2007). Simple behavioural rules may also explain why individuals of many species refrain from
251 breeding in their natal groups, sometimes regardless of whether or not this group contains unrelated
252 immigrants (Harrison et al. 2013a).

253 When Koenig and Haydock (2004) reviewed inbreeding in cooperative breeders, there were
254 no convincing cases of kin recognition more sophisticated than rejecting familiar natal group-
255 members as mates. However, since then, evidence has emerged that direct cues to genetic
256 relatedness exist in many species including cooperative breeders and other group-living species (e.g.
257 cooperatively breeding meerkats (Leclaire et al. 2013); *Neolamprologus pulcher* cichlids (Le Vin,
258 Mable & Arnold 2010) and bell miners *Manorina melanophrys* (McDonald & Wright 2011); and
259 group-living Belding's ground squirrels *Urocitellus beldingi* (Mateo 2010) and zebrafish *Danio rerio*,
260 (Gerlach & Lysiak 2006)). Such mechanisms are likely to be involved in inbreeding avoidance and can
261 be effective even without environmental and social cues to relatedness. Direct cues may therefore
262 be particularly important in promiscuous species where social cues are of limited use (Hain & Neff
263 2006), but may also occur in monogamous species where there are benefits. For example, in the
264 nepotistic (but not cooperatively breeding) Siberian jay *Perisoreus infaustus*, dominant breeders vary
265 in their level of aggression towards unfamiliar immigrants depending on their level of genetic
266 relatedness, implying that genetic kin recognition is involved (Griesser et al. 2015).

267 Direct cues to relatedness are thought to occur primarily via phenotype matching, which can
268 be either self-referent or referent to their mother or siblings and learned during infancy. In self-
269 referent phenotype matching, individuals recognise their own phenotype and assess other
270 individuals on degree of similarity to themselves. This appears to occur in house mice *Mus musculus*
271 *domesticus* (Sherborne *et al.* 2007) and bluegill sunfish *Lepomis macrochirus* (Hain & Neff 2006),
272 neither of which are regular cooperative breeders, but both species sometimes rear broods of mixed
273 parentage. It is also possible that 'recognition alleles' exist, as proposed by Hamilton (1964) and
274 extended into the 'green beard effect' by Dawkins (1979), but the existence of such alleles in
275 vertebrates has been very difficult to test and currently lacks direct evidence (Tang-Martinez 2001,
276 Leclaire *et al.* 2013), but see (Gardner & West 2010).

277 In many vertebrates, direct kin-recognition involves the use of chemical cues. For example,
278 in cooperatively breeding meerkats (Leclaire *et al.* 2013), individuals are able to discriminate
279 between anal gland odours of unfamiliar relatives and non-relatives, while in cooperatively breeding
280 cichlids, individuals associate with others based on chemical cues to relatedness (Le Vin *et al.* 2010).
281 In humans *Homo sapiens*, body-odour based mate choice has been shown to be associated with
282 both kinship (Weisfeld *et al.* 2003) and genetic diversity (Havlicek & Roberts 2009, Lie, Simmons &
283 Rhodes 2010), particularly at Major Histocompatibility Complex (MHC) loci: genes that are involved
284 in the immune response. The MHC, but not diversity or relatedness at other loci, has also been
285 implicated in mate choice in cooperatively breeding Seychelles warblers. Here, females seek EGP if
286 their social partner has low MHC diversity, which in turn is linked to offspring survival (Brouwer *et al.*
287 2010). Probably one of the best understood species in terms of chemical cues to relatedness is the
288 house mouse. Here, although the MHC may play a part, the primary cue to relatedness appears to
289 come from Major Urinary Proteins (MUPs) which have been shown to strongly influence mating
290 decisions with regards to relatedness (Sherborne *et al.* 2007). It is possible that MUPs are important
291 in identifying relatives in other cooperative species, however the presence of such proteins across a
292 wide range of vertebrates remains to be tested and other phylogenetic groups may use alternative

293 methods to discriminate between kin. For example, studies have failed to find evidence of MUPs in
294 two cooperatively breeding mole-rat species (Hagemeyer *et al.* 2011).

295 There is also evidence that inbreeding avoidance can occur postmating. Although such
296 mechanisms appear relatively common in invertebrates (Tregenza & Wedell 2002), there is currently
297 little evidence from vertebrates (Brekke *et al.* 2011). However, there are some relatively convincing
298 cases. For example, in wild-derived house mice that were experimentally mated to both siblings and
299 unrelated males, unrelated males sired more offspring (Firman & Simmons 2008). Post-copulatory
300 mechanisms could be important in many cooperative breeding species and is likely to provide a
301 fruitful area of future research. In particular, cooperative species where females mate multiply often
302 show patterns consistent with post-copulatory mechanisms of inbreeding avoidance (see section
303 below on extra-group mating). However in field-based studies, it is difficult to exclude the possibility
304 that copulation frequency between males may vary, or that inbreeding depression may cause some
305 offspring to die prior to birth. Although difficult to investigate, laboratory experiments provide a
306 better opportunity to assess the degree to which such patterns are a result of pre or post copulatory
307 mechanisms.

308 ***Extra-group mating***

309 Studies of cooperative breeders, and also of socially monogamous but non-cooperative
310 species, have found that extra-pair or extra-group mates are often less related to females than their
311 within-pair mates (Blomqvist *et al.* 2002, Foerster *et al.* 2003, Bishop, O'Ryan & Jarvis 2007, Brouwer
312 *et al.* 2011), suggesting that extra group paternity (EGP) could be used to avoid inbreeding. In some
313 species, females appear more likely to mate extra-group if their social partner is a relative (meerkats
314 (Leclaire *et al.* 2013) grey crowned babblers *Pomatostomus temporalis* (Blackmore & Heinsohn
315 2008), red-backed fairy-wrens *Malurus melanocephalus* (Varian-Ramos & Webster 2012), red-
316 winged fairy-wrens *Malurus elegans* (Brouwer *et al.* 2011) and purple-crowned fairy-wrens *Malurus*
317 *coronatus* (Kingma, Hall & Peters 2013)), suggesting that seeking EGP may be an adaptive strategy to

318 avoid inbreeding when there are constraints on social mate choice. This possibility is supported by a
319 recent meta-analysis across birds (Arct, Drobniak & Cichoń 2015), but inbreeding avoidance may be
320 a particularly important factor driving EGP in cooperative breeders, where populations are
321 particularly viscous and so individuals may be restricted in their choice of social partners (Brouwer et
322 al. 2011).

323 Note that, whilst there is convincing evidence that EGP is used to avoid inbreeding in some
324 species, the generality of EGP as an inbreeding avoidance strategy has been questioned for several
325 reasons. First, in some species, direct fitness benefits may drive the evolution of EGP, for example
326 the paternity confusion caused by multiple mating may reduce infanticide (reviewed by Lukas and
327 Huchard (2014)). Females may also seek 'good genes' for their offspring and so favour males with
328 particular traits (reviewed by Jennions and Petrie (2000)) and EGP may also occur for non-adaptive
329 reasons such as genetic constraints whereby the alleles associated with extra-pair mating are
330 selected for their positive impact on other traits (Forstmeier *et al.* 2014). Second, in some
331 cooperative breeders, population viscosity may reduce the effectiveness of EGP as a way to avoid
332 inbreeding. In the white-browed sparrow weaver *Plocepasser mahali*, extra-group mates were more
333 closely related to females than their social mates (Harrison *et al.* 2013b). The authors suggest that
334 the presence of relatives in the local population may restrict opportunities for inbreeding avoidance,
335 and instead male-male competition may be driving patterns in EGP in this species. Future meta-
336 analyses, focused on cooperative breeders, will be necessary to properly evaluate the evidence for
337 EGP as a method of inbreeding avoidance and to investigate the factors driving variance in the use of
338 EGP across cooperative breeders.

339 **Why is inbreeding not always avoided?**

340 Given the mechanisms of inbreeding avoidance that animals appear to have at their disposal,
341 it is perhaps surprising that inbreeding occurs at all. However, it is important to recognise that both
342 inbreeding and inbreeding avoidance are likely to have costs, and how these balance against each

343 other appears to result in substantial variation in inbreeding rates between individuals, populations
344 and species. Furthermore, in some situations constraints against inbreeding avoidance may apply,
345 whilst in others there may be active benefits of inbreeding, although this possibility remains
346 controversial.

347 One reason why inbreeding may not be avoided in some populations is that the costs of
348 inbreeding may be particularly low. Inbreeding depression appears to have a strong environmental
349 component, with greater effects under more adverse conditions (Armbruster & Reed 2005). For
350 example, in the Seychelles warbler, females with low genetic heterozygosity (hence are likely to
351 display inbreeding depression) produce offspring with lower survival chances, but only in years
352 where survivorship is poor in the population generally (Brouwer, Komdeur & Richardson 2007).
353 Cross-fostering showed that this is not the result of poor maternal care as survival was unrelated to
354 the foster mother's genetic heterozygosity (Brouwer et al. 2007). Among cooperative breeders, the
355 social environment is likely to have a large impact on offspring fitness. It is therefore feasible that
356 helper contributions to care could to some extent offset the negative impacts of inbreeding
357 depression. Such a relationship has been shown in non-cooperative burying beetles *Nicrophorus*
358 *vespilloides*, where maternal care increases the survival of inbred offspring to a greater extent than
359 outbred offspring (Pilakouta *et al.* 2015). However, the possibility that helpers buffer the effects of
360 inbreeding depression has rarely been tested in cooperative vertebrates (but see Nielsen et al.
361 (2012)) and is likely to provide a fruitful area of future research.

362 In species or populations that have undergone frequent inbreeding in the past, the impact of
363 inbreeding depression may be reduced through so-called 'genetic purging', whereby the increased
364 homozygosity resulting from inbreeding exposes recessive deleterious alleles to natural selection,
365 thereby purging them from the genome (Keller & Waller 2002). Further inbreeding would then cause
366 little or no reduction in fitness. While this possibility has received some support in laboratory
367 experiments (Crnokrak & Barrett 2002), its effect in most wild populations is likely to be relatively

368 minor due to a variety of factors including genetic overdominance, immigration and large population
369 sizes (Keller & Waller 2002, Edmands 2007). So far, there is little evidence of purging in wild
370 cooperatively breeding vertebrates, even in those where inbreeding occurs frequently. For example,
371 there is evidence of inbreeding depression in banded mongooses, which regularly inbreed
372 (Sanderson *et al.* 2015).

373 In some species, inbreeding may occur relatively frequently due to constraints on mate
374 choice and dispersal. In the naked mole-rat, dispersal is particularly constrained due to its
375 subterranean desert habitat, where dispersal above ground is extremely hazardous (Bennett &
376 Faulkes 2000). Although outbreeding is preferred and new colonies are formed by large ‘disperser’
377 morphs, which breed away from their natal group (Ciszek 2000), close inbreeding may be tolerated
378 in colonies where one or both of the founding breeders have died (Ingram *et al.* 2015). Here, the
379 costs of abandoning large, successful colonies and dispersing upon breeder death may outweigh the
380 costs of inbreeding. Similarly, in the banded mongoose, the costs of dispersal are high as members
381 of newly founded groups suffer an annual adult mortality rate (0.33) almost three times that of
382 resident groups (0.12) (Cant, Vitikainen & Nichols 2013), whilst the costs of seeking extra-group
383 paternity are high due to aggressive encounters with rival groups which account for the deaths of 20%
384 of pups and 12% of adults (Nichols *et al.* 2015). Here, individuals often remain and breed in their
385 natal groups for their entire lives which results in an increase in inbreeding levels as groups age
386 (Nichols *et al.* 2014). This occurs despite the presence of inbreeding depression in pups, suggesting
387 that the costs of inbreeding avoidance sometimes outweigh the benefits in this species (Sanderson
388 *et al.* 2015).

389 One further suggestion for why some species may tolerate inbreeding is that it may confer
390 benefits under some circumstances. First, inbreeding could act to preserve beneficial clusters of co-
391 adapted genes, which could be broken up by breeding with unrelated mates, thereby leading to
392 selection for an optimal level of inbreeding (Bateson 1983). In support of this idea, Helgason *et al.*

393 (2008) found that the fertility of human couples was highest when they were related at the level of
394 3rd and 4th cousins, although they were not able to explicitly test the mechanism behind this. Second,
395 there may be kin-selected benefits of inbreeding as the offspring of inbred matings are more closely
396 related to their parents due to their inheritance of alleles identical by descent from both parents
397 (Puurtinen 2011, Szulkin et al. 2013). Theoretical work predicts that the net kin-selected benefits of
398 inbreeding will be high when inbreeding depression is low and that such benefits are likely to vary
399 between the sexes and depending on the mating system (Waser, Austad & Keane 1986), potentially
400 creating sexual conflict (Szulkin et al. 2013). Recent extensions to this theoretical work consider
401 simultaneous versus sequential mate choice and relative investment in parental care, and suggest
402 that inbreeding should be tolerated under a wider range of inbreeding depression values than
403 previously thought (Kokko & Ots 2006). Among cooperative breeders, there could be additional
404 benefits of increased relatedness among groups as it may also promote kin-selected helping
405 behaviour, but despite this, the evidence that inbreeding is favoured in either cooperative or non-
406 cooperative vertebrates is scarce (Kokko & Ots 2006). The best evidence comes from a cichlid with
407 biparental care, *Pelvicachromis taeniatus*, where laboratory experiments showed that both sexes
408 prefer mating with unfamiliar close kin over non-kin, and inbred pairs were more cooperative and
409 invested more in their offspring than unrelated parents (Thunken et al. 2007). The source population
410 for the cichlids used in the experiment was relatively small, isolated and had low genetic diversity,
411 presenting the possibility that this population has undergone the purging of deleterious alleles and
412 therefore a reduction of the costs of inbreeding (Langen *et al.* 2011), although this remains to be
413 tested explicitly. A small number of studies have also reported higher relatedness in extra-group
414 mates than within-group mates, which could result from inbreeding preference (Wang & Lu 2011,
415 Harrison et al. 2013b). For example, in cooperative breeding ground tits *Parus humilis*, although
416 social pairs were unrelated, extra-pair mates were relatives (mean $r = 0.137$) (Wang & Lu 2011). As
417 no evidence of inbreeding depression via reduced offspring weight was found, the authors suggest
418 that inbreeding occurs as a result of the kin-selected benefits of providing relatives with mating

419 opportunities. The authors were able to exclude the possibility that inbreeding occurs due to
420 increased relatedness of local mates, which may explain high relatedness in extra-pair mates of
421 white-browed sparrow weavers (Harrison et al. 2013b).

422 It is possible that the general mismatch between theoretical work, which predicts that
423 inbreeding tolerance will occur relatively commonly (Kokko & Ots 2006, Puurtinen 2011) and
424 empirical work, which rarely finds evidence of inbreeding preference, is due to an underestimation
425 by theorists of the effects of inbreeding depression in the wild. The majority of studies on inbreeding
426 depression measure a selection of early-life traits and few consider lifetime breeding success. Future
427 studies using long-term life-history data combined with powerful techniques to detect inbreeding,
428 such as the large panel of single nucleotide polymorphisms (SNPs) used in Huisman et al. (2016),
429 may reveal higher levels of inbreeding depression than previously thought. Alternatively, conditions
430 favouring low levels of inbreeding tolerance may be common in nature. For example, in cases where
431 the costs of choosing an unrelated mate are high. Also, species in which both sexes invest in
432 offspring approximately equally and fairly substantially, and where mate encounter rate is high, are
433 predicted to have some degree of inbreeding tolerance (Kokko & Ots 2006), and these conditions
434 may occur in some cooperatively breeding species. Another possibility is that mating patterns
435 resulting in regular inbreeding may be relatively common but researchers are reluctant to interpret
436 this as evidence for inbreeding tolerance or preference, perhaps due to a lack of awareness of
437 theoretical predictions (Kokko & Ots 2006). Instead, such mating patterns are generally interpreted as
438 occurring due to constraints against inbreeding avoidance (Kokko & Ots 2006, Szulkin et al. 2013).
439 Those conducting studies on inbreeding should therefore consider the possibility that inbreeding
440 may be preferred under some circumstances. Further work is necessary to shed light on the
441 mismatch between theoretical and empirical studies of inbreeding tolerance, and should include
442 both of these types of approach.

443 **The consequences of inbreeding tolerance and avoidance**

444 Many behavioural strategies have evolved to avoid the negative consequences of inbreeding,
445 including dispersal (Koenig, Haydock & Stanback 1998, Griffin *et al.* 2003), reproductive restraint
446 (Cooney & Bennett 2000, Clutton-Brock *et al.* 2001b), the immigration of non-relatives (Koenig *et al.*
447 1998) and extra-group copulations (Brouwer *et al.* 2011). All of these behaviours in turn feed back
448 into group and population structure, influencing the dynamics of the population as a whole (Nichols
449 *et al.* 2012).

450 One of the defining characteristics of cooperative breeding systems is the presence of
451 subordinate helpers that rarely (if ever) breed but instead help to rear the offspring of others.
452 Originally, it was thought that the primary reason for the lack of breeding among subordinates is due
453 to reproductive suppression from dominant breeders (Emlen 1982), and many theoretical models of
454 reproductive skew are based on this assumption (reviewed in Hager and Jones (2009)). However,
455 reproductive skew can also be increased via inbreeding avoidance. For example, in Damaraland
456 mole-rats *Fukomys damarensis*, colonies contain only one female breeder and subordinate females
457 are usually her daughters. Subordinates usually show little or no signs of reproductive behaviour,
458 however when unrelated males are experimentally introduced to a colony, subordinate females
459 show physiological and behavioural signs of sexual activity and often breed with the introduced male
460 (Cooney & Bennett 2000). Subordinate restraint based on inbreeding avoidance may be particularly
461 likely to be found in species where extra-group mating is difficult (Koenig & Haydock 2004), as is
462 likely to be the case in mole-rats, which live in subterranean burrows and rarely venture above
463 ground (Bennett & Faulkes 2000). Similar patterns have been shown in other species, and a large
464 body of evidence now exists to demonstrate the importance of inbreeding avoidance in determining
465 reproductive skew (reviewed in Koenig and Haydock (2004)). Nevertheless, inbreeding avoidance is
466 still rarely considered in theoretical models of reproductive skew (reviewed in Hager and Jones
467 (2009)).

468 Inbreeding avoidance via female promiscuity is likely to impact on helping behaviour. Unless
469 the extra-pair or extra-group male is related to the within-group male breeder, EGP will likely reduce
470 relatedness between group-members and hence may have a negative impact on helping effort.
471 Although this possibility has not been tested directly, it has been shown that even fine-scale
472 differences in relatedness to the brood can impact on helping rates (e.g. bell miners *Manorina*
473 *melanophrys* (Wright *et al.* 2009)). In Seychelles warblers, helping behaviour has been linked to EGP
474 as female helpers use the presence of their mother but not their social fathers (i.e. the dominant
475 male present on the territory where they hatched) as a cue to help, as the high level of EGP means
476 that the social father may well not be a relative (Komdeur *et al.* 2004). This may result in a reduction
477 or absence of helping behaviour if the female breeder on a territory dies, regardless of whether or
478 not the genetic father is still present.

479 Although relatedness to young does not always impact on individual decisions of whether to
480 provide help (Clutton-Brock *et al.* 2001a), comparative studies across birds and mammals find that
481 relatedness between group members is important in the evolution of cooperative breeding (Griffin
482 & West 2003). It is therefore likely that the method of inbreeding avoidance that a species uses
483 directly influences whether or not that species evolves cooperative breeding, via its influence on
484 relatedness. In species where subordinates avoid inbreeding by restraint, reproductive skew is likely
485 to be high and monogamy may be the most likely mating system. Phylogenetic analyses have indeed
486 shown that monogamy promotes the evolution of cooperative breeding through increasing within-
487 group relatedness (Cornwallis *et al.* 2010, Lukas & Clutton-Brock 2012). Conversely, inbreeding
488 avoidance via promiscuity reduces within-group relatedness and is therefore likely to lead to the loss
489 of cooperative breeding over evolutionary time (Cornwallis *et al.* 2010, Lukas & Clutton-Brock 2012).

490 Inbreeding may have additional impacts on helping behaviour besides influencing
491 relatedness within groups. Those studying helping behaviour have often remarked on the high level
492 of individual differences in contributions to cooperative activities (Bergmüller, Schürch & Hamilton

2010, English, Nakagawa & Clutton-Brock 2010). Some of these differences can be explained by differences in the relative costs and benefits of helping which co-varies with factors including (but not limited to) age, sex and condition as well as relatedness (reviewed in (Heinsohn & Legge 1999, Russell 2004). However, much variation in helping effort remains unexplained. It is possible that inbreeding may play a part; if inbred individuals are of lower quality than outbred individuals, inbreeding may lead to a reduction in propensity to help. Alternatively, inbred individuals may be poor competitors over reproductive opportunities, and may therefore increase their input into help thus gaining indirect fitness benefits. Although these possibilities have not been tested explicitly (but see tentative evidence from Nielsen (2013)), studies have shown that inbreeding depression impacts on body condition (Keller & Waller 2002), and condition in turn influences cooperation (Clutton-Brock *et al.* 2002, van de Crommenacker, Komdeur & Richardson 2011), therefore providing a plausible mechanism for inbreeding effects.

505

Finally, both inbreeding and inbreeding avoidance in cooperatively breeding species are likely to have implications for population growth and viability, and therefore may be of particular interest in species of conservation concern. Anthropogenic habitat fragmentation often constrains dispersal and hence can lead to increased levels of inbreeding and inbreeding depression (Edmands 2007). In this situation, conservationists may attempt ‘genetic rescue’ whereby unrelated individuals are introduced from another population, an approach that has proved to be successful for several species (Edmands 2007). Such translocations also risk inducing outbreeding depression if the population exhibits some degree of local adaptation, however the costs of inbreeding are likely to outweigh the risk of outbreeding depression in the majority of cases.

515

The effects of inbreeding and outbreeding are likely to be important in the conservation management of all species, but cooperative breeders require additional consideration. For example, when making predictions about population viability, conservationists often make the assumption of

519 random mating, however the assumption is unlikely to be valid in species with additional kin
520 recognition mechanisms, such as occurs in many cooperative breeders (Jamieson et al. 2009). Here,
521 inbreeding avoidance can reduce opportunities for breeding and so can lead to substantial
522 population declines by lowering the effective population size. For example, in a reintroduced
523 population of ~220 African wild dogs *Lycaon pictus*, inbreeding avoidance mechanisms have been
524 projected to massively increase population extinction risk from just 1.6 % over 100 years to certain
525 extinction within 19 - 63 years (Becker *et al.* 2012). In the acorn woodpecker *Melanerpes*
526 *formicivorus*, inbreeding avoidance means that breeding vacancies that arise after the death of a
527 dominant often remain unfilled, leading to a reduction in the reproductive potential by 9-12%,
528 representing a ~2% annual decline in population growth (Koenig, Stanback & Haydock 1999). In such
529 species, it may be worth considering employing additional measures to increase encounter rate with
530 unrelated individuals such as increasing habitat connectivity or, where this is not possible, moving
531 dispersers between populations.

532

533 **Conclusion**

534 Although the issue of inbreeding has been a subject of great historical interest, we have
535 achieved a much better understanding of its extent, consequences, and the mechanisms by which it
536 acts in the last 13 years. In particular, cooperative breeding systems evolve and are shaped by many
537 factors linked to inbreeding such as relatedness and population dynamics. Consequently, not only
538 are cooperative breeders particularly tractable systems for many remaining questions in the study of
539 inbreeding more generally, but they also present many unique questions and challenges that will
540 lead to a much better understanding of the link between genetic and social attributes of a
541 population. Finally, the information gained from such studies will be important not only from an
542 academic perspective, but also promises to inform conservation programmes for cooperative
543 species.

Box 2. Measuring inbreeding

Pedigrees: A common way to investigate the frequency, distribution and consequences of inbreeding is to use a pedigree. This approach requires accurate parentage assignments, which generally requires genetic parentage analysis, at least to determine paternity. Parentage is usually assigned using a panel of 5-30 microsatellites; short repetitive sequences of DNA that occur throughout the genome. Microsatellites provide an ideal genetic marker for parentage assignment because the laboratory work involved is relatively cost-effective, they provide single locus information, are codominant, are highly variable, and can be amplified from relatively poor-quality DNA allowing non-invasive sampling techniques (Pemberton 2008). Parentage analysis can then be conducted using a variety of computer programmes including Cervus (Marshall *et al.* 1998), Colony (Wang & Santure 2009), and MasterBayes (Hadfield 2009) which is implemented in statistical programme R. Pemberton (2008) and Walling *et al.* (2010) provide further details on these programmes and their respective advantages and disadvantages. Once a pedigree has been constructed, the inbreeding coefficient (f) of each individual can be estimated. An f of 0.25 indicates close inbreeding while an f of 0.125 indicates moderate inbreeding (see Box 1). f values can be estimated from pedigrees, even when the pedigree is incomplete (very few pedigrees derived from wild populations have parentage assigned to all individuals (Marshall *et al.* 2002)), but pedigree depth, accuracy and structure must be taken into account when performing downstream analyses (Pemberton 2008).

Genetic markers: When it is not possible to generate a pedigree, for example when long-term life-history data is not available, a panel of microsatellites can be used to directly estimate inbreeding. Inbred individuals are expected to be less genetically diverse (heterozygous) than

546

Box 2 cont.

547

outbred individuals so inbreeding depression can be assessed through investigating associations between heterozygosity and fitness-related traits (known as heterozygosity-fitness correlations (HFCs)). The relative ease of this approach has resulted in a large number of studies investigating HFCs, many of which find positive associations (reviewed by Lehmann and Perrin (2003), Pemberton (2008), Chapman *et al.* (2009), Szulkin, Bierne and David (2010)). However, the effectiveness of this approach has been called into question as the correlation between inbreeding coefficient and microsatellite heterozygosity is often low (Balloux, Amos & Coulson 2004, Pemberton 2008, Szulkin *et al.* 2010). Nevertheless, where inbreeding is relatively common (for example due to disassortative mating between relatives, small population sizes, bottlenecks, admixture or immigration), HFCs may be detectable using microsatellites (Szulkin *et al.* 2010), especially where a large panel of markers is used (Stoffel *et al.* 2016). Furthermore, where HFCs have been found, there has also been debate about their cause. Although they may be a result of an effect of genome-wide heterozygosity on fitness (known as general effects), they can also result from linkage between a single locus and a fitness trait (known as local effects) (however, small microsatellite datasets are rarely suitable for the detection of local effects, reviewed in Pemberton (2004), Szulkin *et al.* (2010)).

As the ability of genetic markers to detect inbreeding increases with the number of markers used (Hoffman 2014), more recent studies have used genomic data such as large panels of **single nucleotide polymorphisms (SNPs)** to investigate inbreeding (e.g. over 10 000 individual SNPs) (reviewed in (Kardos *et al.* 2016)). With such a large number of markers, heterozygosity correlates well with pedigree inbreeding and the problem of local effects driving HFCs disappears (Heinsohn & Legge 1999, Hoffman *et al.* 2014). Although currently limited by expense, genomic methods have been shown to reveal inbreeding depression in cases where pedigrees have failed to do so, such as in (non-cooperative) deer and sheep (Bérénos *et al.* 2016, Huisman *et al.* 2016). Similar genomic studies in cooperative breeders will provide much greater power in quantifying inbreeding and its effects.

Box 2. Cont.

Measuring population-level inbreeding: Some studies estimate the level of inbreeding in a population by calculating Wright's F-statistics using a panel of genetic markers (usually microsatellites). Three F-statistics are commonly calculated (1) F_{ST} : the degree of reduction in heterozygosity of subpopulations due to population subdivision, (2) F_{IS} : the reduction in heterozygosity of individuals relative to their subpopulation, caused by non-random mating within subpopulations, and (3) F_{IT} : the reduction in heterozygosity of individuals relative to the entire population. Note that such statistics do not measure individual-level inbreeding and hence caution should be applied when interpreting them and statements such as 'F_{IS} was zero, hence there was no evidence for inbreeding in the population' are misleading (Keller & Waller 2002). Instead, an F_{IS} of zero simply suggests random mating within the subpopulation, and is not equivalent to finding a lack of mating between relatives using a pedigree. Interpreting F-statistics may be particularly challenging for species with complex social and/or mating systems (as many cooperative breeders do). As an example, banded mongoose social groups have significantly negative F_{IS} values and F_{IT} values close to zero (Nichols *et al.* 2012), which could be interpreted as outbreeding within groups and low levels of inbreeding in the population. However, a pedigree of the same population reveals high levels of inbreeding, with 8% of pups being the product of close inbreeding and 27% of pups being the product of moderate inbreeding (Nichols *et al.* 2014).

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883

884



885 **Figures**

886

887 Figure 1. Two closely related species (family Herpestidae) with contrasting patterns of inbreeding.
888 The banded mongoose (a) shows low reproductive skew within groups and high levels of natal
889 philopatry with both sexes frequently breeding within natal groups. This results in relatively high
890 levels of close and moderate inbreeding (8% and 27% pups respectively) (Nichols et al. 2014). The
891 meerkat (b) shows high reproductive skew within groups, with natal subordinate females breeding
892 occasionally with immigrant males. Here, close inbreeding is absent and moderate inbreeding occurs
893 in 6.6% of the population, almost always occurring between unfamiliar relatives from different natal
894 groups (Nielsen et al. 2012).

895