# The causes and consequences of inbreeding avoidance and tolerance in cooperatively breeding vertebrates

Hazel J Nichols

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

Liverpool, L3 3AF

h.j.nichols@ljmu.ac.uk

**Short title:** Inbreeding in cooperative breeders

**Abstract**

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

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

## Introduction

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

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

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

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

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

In this review, I first highlight why inbreeding and inbreeding avoidance are of particular interest in cooperatively breeding species. I then go on to evaluate the prevalence and distribution of inbreeding among cooperative species, before exploring ways through which inbreeding is avoided, and why some species may tolerate frequent inbreeding. Following this, I discuss the consequences of inbreeding avoidance and tolerance for cooperative breeders. Finally, I outline 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.

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

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

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

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

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

## How is inbreeding avoided?

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

### *Dispersal*

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

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

***Kin recognition***

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

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

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

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

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

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

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

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

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

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

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

**Why is inbreeding not always avoided?**

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

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

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

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

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

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

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

**The consequences of inbreeding tolerance and avoidance**

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

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

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

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

Inbreeding may have additional impacts on helping behaviour besides influencing relatedness within groups. Those studying helping behaviour have often remarked on the high level 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.

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.

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

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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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550 **References**


551 Aranzamendi, N. H., M. L. Hall, S. A. Kingma, P. Sunnucks & A. Peters (2016) Incest avoidance,
552 extrapair paternity, and territory quality drive divorce in a year-round territorial bird.
553 *Behavioral Ecology,* **27,** 1808-1819.
554 Archie, E. A., J. A. Hollister-Smith, J. H. Poole, P. C. Lee, C. J. Moss, J. E. Maldonado, R. C. Fleischer & S.
555 C. Alberts (2007) Behavioural inbreeding avoidance in wild African elephants. *Molecular*
556 *Ecology,* **16,** 4138-4148.
557 Arct, A., S. M. Drobniak & M. Cichoń (2015) Genetic similarity between mates predicts extrapair
558 paternity—a meta-analysis of bird studies. *Behavioral Ecology,* **26,** 959-968.
559 Armbruster, P. & D. Reed (2005) Inbreeding depression in benign and stressful environments.
560 *Heredity,* **95,** 235-242.
561 Balloux, F., W. Amos & T. N. Coulson (2004) Does heterozygosity estimate inbreeding in real
562 populations? *Molecular Ecology,* **13,** 3021-3031.
563 Bateson, P. (1983) Optimal outbreeding. *Mate choice,* **257,** 277.
564 Becker, P. A., P. S. Miller, M. S. Gunther, M. J. Somers, D. E. Wildt & J. E. Maldonado (2012)
565 Inbreeding avoidance influences the viability of reintroduced populations of African wild
566 dogs (Lycaon pictus). *PloS one,* **7,** e37181.
567 Bennett, N. C. & C. G. Faulkes (2000) *African mole-rats, ecology and eusociality*. Cambridge, UK:
568 Cambridge University Press.
569 Bérénos, C., P. A. Ellis, J. G. Pilkington & J. M. Pemberton (2016) Genomic analysis reveals depression
570 due to both individual and maternal inbreeding in a free-living mammal population.
571 *Molecular Ecology,* **25,** 3152–3168
572 Bergmüller, R., R. Schürch & I. M. Hamilton (2010) Evolutionary causes and consequences of
573 consistent individual variation in cooperative behaviour. *Philosophical Transactions of the*
574 *Royal Society B: Biological Sciences,* **365,** 2751-2764.
575 Bishop, J. M., C. O'Ryan & J. U. Jarvis (2007) Social common mole-rats enhance outbreeding via
576 extra-pair mating. *Biology Letters,* **3,** 176-179.
577 Blackmore, C. J. & R. Heinsohn (2008) Variable mating strategies and incest avoidance in
578 cooperatively breeding grey-crowned babblers. *Animal Behaviour,* **75,** 63-70.
579 Blomqvist, D., M. Andersson, C. Küpper, I. C. Cuthill, J. Kis, R. B. Lanctot, B. K. Sandercock, T. Székely,
580 J. Wallander & B. Kempenaers (2002) Genetic similarity between mates and extra-pair
581 parentage in three species of shorebirds. *Nature,* **419,** 613-615.
582 Braude, S. (2000) Dispersal and new colony formation in wild naked mole-rats: evidence against
583 inbreeding as the system of mating. *Behavioral Ecology,* **11,** 7-12.
584 Brekke, P., J. Wang, P. M. Bennett, P. Cassey, D. A. Dawson, G. J. Horsburgh & J. G. Ewen (2011)
585 Postcopulatory mechanisms of inbreeding avoidance in the island endemic hihi (Notiomystis
586 cincta). *Behavioral Ecology,* **23,** 278-284.
587 Brouwer, L., I. Barr, M. Van De Pol, T. Burke, J. Komdeur & D. S. Richardson (2010) MHC-dependent
588 survival in a wild population: evidence for hidden genetic benefits gained through extra-pair
589 fertilizations. *Molecular Ecology,* **19,** 3444-3455.
590 Brouwer, L., J. Komdeur & D. S. Richardson (2007) Heterozygosity-fitness correlations in a
591 bottlenecked island species: a case study on the Seychelles warbler. *Molecular Ecology,* **16,**
592 3134-3144.
593 Brouwer, L., M. Van De Pol, E. L. S. Atema & A. Cockburn (2011) Strategic promiscuity helps avoid
594 inbreeding at multiple levels in a cooperative breeder where both sexes are philopatric.
595 *Molecular Ecology,* **20,** 4796-4807.
596 Brzeski, K. E., D. R. Rabon, M. J. Chamberlain, L. P. Waits & S. S. Taylor (2014) Inbreeding and
597 inbreeding depression in endangered red wolves (Canis rufus). *Molecular ecology,* **23,** 4241-
598 4255.

599 Burland, T. M., N. C. Bennett, J. U. M. Jarvis & C. G. Faulkes (2002) Eusociality in African mole-rats:
600 new insights from patterns of genetic relatedness in the Damaraland mole-rat (Cryptomys
601 damarensis). *Proceedings of the Royal Society of London. Series B, Biological Sciences,* **269,**
602 1025-1030.
603 Cant, M. A., S. J. Hodge, M. B. V. Bell, J. S. Gilchrist & H. J. Nichols (2010) Reproductive control via
604 eviction (but not the threat of eviction) in banded mongooses. *Proceedings of the Royal*
605 *Society of London. Series B, Biological Sciences,* **277,** 2219-2226.
606 Cant, M. A., E. Vitikainen & H. J. Nichols (2013) Demography and Social Evolution of Banded
607 Mongooses. *Advances in the Study of Behavior, Vol 45,* **45,** 407-445.
608 Chapman, J., S. Nakagawa, D. Coltman, J. Slate & B. Sheldon (2009) A quantitative review of
609 heterozygosity–fitness correlations in animal populations. *Molecular Ecology,* **18,** 2746-2765.
610 Charlesworth, D. & B. Charlesworth (1987) Inbreeding depression and its evolutionary consequences.
611 *Annual review of ecology and systematics***,** 237-268.
612 Charlesworth, D. & J. H. Willis (2009) The genetics of inbreeding depression. *Nat Rev Genet,* **10,** 783-
613 796.
614 Ciszek, D. (2000) New colony formation in the "highly inbred" eusocial naked mole-rat: outbreeding
615 is preferred. *Behavioral Ecology,* **11,** 1-6.
616 Clutton-Brock, T. H. (1989) Female transfer and inbreeding avoidance in social mammals. *Nature,*
617 **337,** 70-72.
618 Clutton-Brock, T. H., P. N. M. Brotherton, M. J. O'Riain, A. S. Griffin, D. Gaynor, R. Kansky, L. L. Sharpe
619 & G. M. McIlrath (2001a) Contributions to cooperative rearing in meerkats. *Animal*
620 *Behaviour,* **61,** 705-710.
621 Clutton-Brock, T. H., P. N. M. Brotherton, A. F. Russell, M. J. O'Riain, D. Gaynor, R. Kansky, A. Griffin,
622 M. Manser, L. Sharpe, G. M. McIlrath, T. Small, A. Moss & S. Monfort (2001b) Cooperation,
623 control and concession in meerkat groups. *Science,* **291,** 478-481.
624 Clutton-Brock, T. H., S. J. Hodge, T. P. Flower, G. F. Spong & A. J. Young (2010) Adaptive suppression
625 of subordinate reproduction in cooperative mammals. *The American Naturalist,* **176,** 664-
626 673.
627 Clutton-Brock, T. H. & D. Lukas (2012) The evolution of social philopatry and dispersal in female
628 mammals. *Molecular Ecology,* **21,** 472-492.
629 Clutton-Brock, T. H., A. F. Russell, L. L. Sharpe, A. J. Young, Z. Balmforth & G. M. McIlrath (2002)
630 Evolution and development of sex differences in cooperative behavior in meerkats. *Science,*
631 **297,** 253-256.
632 Cockburn, A., H. L. Osmond, R. A. Mulder, D. J. Green & M. C. Double (2003) Divorce, dispersal and
633 incest avoidance in the cooperatively breeding superb fairy-wren Malurus cyaneus. *Journal*
634 *of Animal Ecology,* **72,** 189-202.
635 Cooney, R. & N. C. Bennett (2000) Inbreeding avoidance and reproductive skew in a cooperative
636 mammal. *Proceedings of the Royal Society of London B: Biological Sciences,* **267,** 801-806.
637 Cornwallis, C. K., S. A. West, K. E. Davis & A. S. Griffin (2010) Promiscuity and the evolutionary
638 transition to complex societies. *Nature,* **466,** 969-972.
639 Craig, J. L. & I. G. Jamieson (1988) Incestuous mating in a communal bird: a family affair. *American*
640 *Naturalist,* **131,** 58-70.
641 Crnokrak, P. & S. C. Barrett (2002) Perspective: purging the genetic load: a review of the
642 experimental evidence. *Evolution,* **56,** 2347-2358.
643 Daniels, S. J. & J. R. Walters (2000) Between-year breeding dispersal in red-cockaded woodpeckers:
644 multiple causes and estimated cost. *Ecology,* **81,** 2473-2484.
645 Darwin, C., (1900) The effects of cross and self fertilisation in the vegetable kingdom. J. Murray,
646 London.
647 Dawkins, R. (1979) Twelve misunderstandings of kin selection. *Zeitschrift für Tierpsychologie,* **51,**
648 184-200.

649 Dickinson, J., Ç. Akçay, E. D. Ferree & C. A. Stern, (2016) Western bluebirds: Lessons from a marginal
650 cooperative breeder. In: *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution,*
651 *and Behavior*: 19. W. Koenig & J. Dickinson (Eds.).
652 Du Plessis, M. A. (1992) Obligate cavity-roosting as a constraint on dispersal of green (red-billed)
653 woodhoopoes: consequences for philopatry and the likelihood of inbreeding. *Oecologia,* **90,**
654 205-211.
655 Edmands, S. (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and
656 outbreeding for conservation and management. *Molecular Ecology,* **16,** 463-475.
657 Emlen, S. T. (1982) The evolution of helping. II. The role of behavioural conflict. *The American*
658 *Naturalist,* **119,** 40-53.
659 English, S., S. Nakagawa & T. Clutton-Brock (2010) Consistent individual differences in cooperative
660 behaviour in meerkats (Suricata suricatta). *Journal of evolutionary biology,* **23,** 1597-1604.
661 Ens, B. J., U. N. Safriel & M. P. Harris (1993) Divorce in the long-lived and monogamous oystercatcher,
662 Haematopus ostralegus: incompatibility or choosing the better option? *Animal Behaviour,* **45,**
663 1199-1217.
664 Firman, R. C. & L. W. Simmons (2008) Polyandry facilitates postcopulatory inbreeding avoidance in
665 house mice. *Evolution,* **62,** 603-611.
666 Fitzpatrick, J. W. & R. Bowman, (2016) Florida Scrub-Jay: Oversized territories and group defense in a
667 fire-maintained habitat. In: *Cooperative Breeding in Vertebrates: Studies of Ecology,*
668 *Evolution, and Behavior*: 77. W. Koenig & J. Dickinson (Eds.).
669 Foerster, K., K. Delhey, A. Johnsen, J. T. Lifjeld & B. Kempenaers (2003) Females increase offspring
670 heterozygosity and fitness through extra-pair matings. *Nature,* **425,** 714-717.
671 Forstmeier, W., S. Nakagawa, S. C. Griffith & B. Kempenaers (2014) Female extra-pair mating:
672 adaptation or genetic constraint? *Trends in Ecology & Evolution,* **29,** 456-464.
673 Gardner, A. & S. A. West (2010) Greenbeards. *Evolution,* **64,** 25-38.
674 Geffen, E., M. Kam, R. Hefner, P. Hersteinsson, A. ANGERBJOeRN, L. Dalen, E. Fuglei, K. Noren, J. R.
675 Adams & J. Vucetich (2011) Kin encounter rate and inbreeding avoidance in canids.
676 *Molecular ecology,* **20,** 5348-5358.
677 Gerlach, G. & N. Lysiak (2006) Kin recognition and inbreeding avoidance in zebrafish, Danio rerio, is
678 based on phenotype matching. *Animal Behaviour,* **71,** 1371-1377.
679 Griesser, M., P. Halvarsson, S. M. Drobniak & C. Vilà (2015) Fine-scale kin recognition in the absence
680 of social familiarity in the Siberian jay, a monogamous bird species. *Molecular Ecology,* **24,**
681 5726-5738.
682 Griffin, A. S., J. M. Pemberton, P. N. M. Brotherton, G. McIlrath, D. Gaynor, R. Kansky, J. O'Riain & T.
683 H. Clutton-Brock (2003) A genetic analysis of breeding success in the cooperative meerkat
684 (*Suricata suricatta*). *Behavioral Ecology,* **14,** 472-480.
685 Griffin, A. S. & S. A. West (2003) Kin discrimination and the benefit of helping in cooperatively
686 breeding vertebrates. *Science,* **302,** 634-636.
687 Hadfield, J., (2009) Package 'MasterBayes'.
688 Hagemeyer, P., S. Begall, K. Janotova, J. Todrank, G. Heth, P. Jedelsky, H. Burda & P. Stopka (2011)
689 Searching for Major Urinary Proteins (MUPs) as Chemosignals in Urine of Subterranean
690 Rodents. *J Chem Ecol,* **37,** 687-694.
691 Hager, R. & C. B. Jones (2009) *Reproductive skew in vertebrates: proximate and ultimate causes.*
692 Cambridge, UK: Cambridge University Press.
693 Hain, T. J. & B. D. Neff (2006) Promiscuity drives self-referent kin recognition. *Current Biology,* **16,**
694 1807-1811.
695 Hamilton, W. D. (1964) The genetical theory of social behaviour I, II. *Journal of Theoretical Biology,* **7,**
696 1-52.
697 Harrison, X. A., J. E. York, D. L. Cram, M. C. Hares & A. J. Young (2013a) Complete reproductive skew
698 within white-browed sparrow weaver groups despite outbreeding opportunities for
699 subordinates of both sexes. *Behavioral Ecology and Sociobiology,* **67,** 1915-1929.

Harrison, X. A., J. E. York, D. L. Cram & A. J. Young (2013b) Extra-group mating increases inbreeding risk in a cooperatively breeding bird. *Molecular Ecology,* **22,** 5700-5715.
Hatchwell, B. J., (2016) Long-tailed tits: Ecological causes and fitness consequences of redirected helping. In: *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior*: 39. W. Koenig & J. Dickinson (Eds.).
Havlicek, J. & S. C. Roberts (2009) MHC-correlated mate choice in humans: a review. *Psychoneuroendocrinology,* **34,** 497-512.
Heinsohn, R. & S. Legge (1999) The cost of helping. *Trends in Ecology & Evolution,* **14,** 53-57.
Helgason, A., S. Pálsson, D. F. Guðbjartsson, þ. Kristjánsson & K. Stefánsson (2008) An Association Between the Kinship and Fertility of Human Couples. *Science,* **319,** 813-816.
Hoffman, J. I., F. Simpson, P. David, J. M. Rijks, T. Kuiken, M. A. Thorne, R. C. Lacy & K. K. Dasmahapatra (2014) High-throughput sequencing reveals inbreeding depression in a natural population. *Proceedings of the National Academy of Sciences,* **111,** 3775-3780.
Huisman, J., L. E. Kruuk, P. A. Ellis, T. Clutton-Brock & J. M. Pemberton (2016) Inbreeding depression across the lifespan in a wild mammal population. *Proceedings of the National Academy of Sciences,* **113,** 3585-3590.
Ihle, M. & W. Forstmeier (2013) Revisiting the evidence for inbreeding avoidance in zebra finches. *Behavioral Ecology,* **24,** 1356-1362.
Ingram, C. M., N. J. Troendle, C. A. Gill, S. Braude & R. L. Honeycutt (2015) Challenging the inbreeding hypothesis in a eusocial mammal: population genetics of the naked mole-rat, Heterocephalus glaber. *Molecular Ecology,* **24,** 4848-4865.
Jamieson, I. G., S. S. Taylor, L. N. Tracy, H. Kokko & D. P. Armstrong (2009) Why some species of birds do not avoid inbreeding: insights from New Zealand robins and saddlebacks. *Behavioral Ecology,* **20,** 575-584.
Jennions, M. D. & M. Petrie (2000) Why do females mate multiply? A review of the genetic benefits. *Biological Reviews,* **75,** 21-64.
Kardos, M., H. R. Taylor, H. Ellegren, G. Luikart & F. W. Allendorf (2016) Genomics advances the study of inbreeding depression in the wild. *Evolutionary Applications,* **9,** 1205-1218.
Keane, B., S. R. Creel & P. M. Waser (1996) No evidence of inbreeding avoidance or inbreeding depression in a social carnivore. *Behavioral Ecology,* **7,** 480-489.
Keller, L. F. & D. M. Waller (2002) Inbreeding effects in wild populations. *Trends in Ecology and Evolution,* **17,** 230-241.
Kingma, S. A., M. L. Hall & A. Peters (2013) Breeding synchronization facilitates extrapair mating for inbreeding avoidance. *Behavioral Ecology,* **24,** 1390-1397.
Koenig, W. & J. Dickinson (2004) *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge, UK: Cambridge University Press.
Koenig, W. & J. Dickinson (2016) *Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior*. Cambridge University Press.
Koenig, W., M. T. Stanback & J. Haydock (1999) Demographic consequences of incest avoidance in the cooperatively breeding acorn woodpecker. *Animal Behaviour,* **57,** 1287-1293.
Koenig, W. D. & J. Haydock, (2004) Incest and incest avoidance. In: *Ecology and Evolution of Cooperative Breeding in Birds.*: 142-156. W. Koenig & J. Dickinson (Eds.). Cambridge University Press, Cambridge.
Koenig, W. D., J. Haydock & M. T. Stanback (1998) Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. *The American Naturalist,* **151,** 243-255.
Kokko, H. & I. Ots (2006) When not to avoid inbreeding. *Evolution,* **60,** 467-475.
Komdeur, J. & B. Hatchwell (1999) Kin recognition: function and mechanism in avian societies. *Trends in Ecology & Evolution,* **14,** 237-241.

749 Komdeur, J., D. S. Richardson & T. Burke (2004) Experimental evidence that kin discrimination in the
750 Seychelles warbler is based on association and not on genetic relatedness. *Proceedings of*
751 *the Royal Society of London, Series B: Biological Sciences,* **271,** 963-969.
752 Kuester, J., A. Paul & J. Arnemann (1994) Kinship, familiarity and mating avoidance in Barbary
753 macaques, Macaca sylvanus. *Animal Behaviour,* **48,** 1183-1194.
754 Langen, K., J. Schwarzer, H. Kullmann, T. C. Bakker & T. Thünken (2011) Microsatellite support for
755 active inbreeding in a cichlid fish. *PLoS One,* **6,** e24689.
756 Le Vin, A., B. Mable & K. Arnold (2010) Kin recognition via phenotype matching in a cooperatively
757 breeding cichlid, Neolamprologus pulcher. *Animal Behaviour,* **79,** 1109-1114.
758 Leclaire, S., J. F. Nielsen, N. K. Thavarajah, M. B. Manser & T. H. Clutton-Brock (2013) Odour-based
759 kin discrimination in the cooperatively breeding meerkat. *Biology letters,* **9,** 20121054.
760 Lehmann, L. & N. Perrin (2003) Inbreeding Avoidance through Kin Recognition: Choosy Females
761 Boost Male Dispersal. *The American Naturalist,* **162,** 638-652.
762 Liberg, O., H. Andrén, H.-C. Pedersen, H. Sand, D. Sejberg, P. Wabakken, M. Åkesson & S. Bensch
763 (2005) Severe inbreeding depression in a wild wolf Canis lupus population. *Biology letters,* **1,**
764 17-20.
765 Lie, H. C., L. W. Simmons & G. Rhodes (2010) Genetic dissimilarity, genetic diversity, and mate
766 preferences in humans. *Evolution and Human Behavior,* **31,** 48-58.
767 Lukas, D. & T. H. Clutton-Brock (2012) Cooperative breeding and monogamy in mammalian societies.
768 *Proceedings of the Royal Society of London. Series B, Biological Sciences,* **279,** 2151-2156.
769 Lukas, D. & E. Huchard (2014) The evolution of infanticide by males in mammalian societies. *Science,*
770 **346,** 841-844.
771 Marshall, T. C., D. W. Coltman, J. M. Pemberton, J. Slate, J. A. Spalton, F. E. Guinness, J. A. Smith, J. G.
772 Pilkinton & T. H. Clutton-Brock (2002) Estimating the prevalence of inbreeding from
773 incomplete pedigrees. *Proceedings of the Royal Society of London. Series B, Biological*
774 *Sciences,* **269,** 1533-1539.
775 Marshall, T. C., J. B. K. E. Slate, L. E. B. Kruuk & J. M. Pemberton (1998) Statistical confidence for
776 likelihood-based paternity inference in natural populations. *Molecular Ecology,* **7,** 639-655.
777 Mateo, J. M. (2010) Self-referent phenotype matching and long-term maintenance of kin recognition.
778 *Animal Behaviour,* **80,** 929-935.
779 McDonald, P. G. & J. Wright (2011) Bell miner provisioning calls are more similar among relatives and
780 are used by helpers at the nest to bias their effort towards kin. *Proceedings of the Royal*
781 *Society of London B: Biological Sciences,* **278,** 3403-3411.
782 McRae, S. B. (1996) Family values: costs and benefits of communal nesting in the moorhen. *Animal*
783 *Behaviour,* **52,** 225-245.
784 Meagher, S., D. J. Penn & W. K. Potts (2000) Male–male competition magnifies inbreeding
785 depression in wild house mice. *Proceedings of the National Academy of Sciences,* **97,** 3324-
786 3329.
787 Moore, J. & R. Ali (1984) Are dispersal and inbreeding avoidance related? *Animal Behaviour,* **32,** 94-
788 112.
789 Nelson-Flower, M. J., P. A. R. Hockey, C. O'Ryan & A. R. Ridley (2012) Inbreeding avoidance
790 mechanisms: dispersal dynamics in cooperatively breeding southern pied babblers. *Journal*
791 *of Animal Ecology,* **81,** 876-883.
792 Nichols, H. J., M. A. Cant, J. I. Hoffman & J. L. Sanderson (2014) Evidence for frequent incest in a
793 cooperatively breeding mammal. *Biology Letters,* **10**.
794 Nichols, H. J., M. A. Cant & J. L. Sanderson (2015) Adjustment of costly extra-group paternity
795 according to inbreeding risk in a cooperative mammal. *Behavioral Ecology,* **26,** 1486-1494.
796 Nichols, H. J., N. R. Jordan, G. A. Jamie, M. A. Cant & J. I. Hoffman (2012) Fine-scale spatiotemporal
797 patterns of genetic variation reflect budding dispersal coupled with strong natal philopatry
798 in a cooperatively breeding mammal. *Molecular Ecology,* **21,** 5348-5362.
799 Nielsen, J. F., (2013) Evolutionary genetics of meerkats (Suricata suricatta). University of Edinburgh.

Nielsen, J. F., S. English, W. P. Goodall-Copestake, J. Wang, C. A. Walling, A. Bateman, T. P. Flower, R. L. Sutcliffe, J. Samson, N. K. Thavarajh, L. E. B. Kruuk, T. H. Clutton-Brock & J. M. Pemberton (2012) Inbreeding and inbreeding depression of early life traits in a cooperative mammal. *Molecular Ecology,* **21,** 2788-2804.

O'Riain, M., N. Bennett, P. Brotherton, G. McIlrath & T. Clutton-Brock (2000) Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (Suricata suricatta). *Behavioral Ecology and Sociobiology,* **48,** 471-477.

Pemberton, J. M. (2004) Measuring inbreeding depression in the wild: the old ways are the best. *Trends in Ecology & Evolution,* **19,** 613-615.

Pemberton, J. M. (2008) Wild pedigrees: the way forward. *Proceedings of the Royal Society of London B: Biological Sciences,* **275,** 613-621.

Pilakouta, N., S. Jamieson, J. A. Moorad & P. T. Smiseth (2015) Parental care buffers against inbreeding depression in burying beetles. *Proceedings of the National Academy of Sciences,* **112,** 8031-8035.

Pusey, A. & M. Wolf (1996) Inbreeding avoidance in animals. *Trends in Ecology and Evolution,* **11,** 201-206.

Puurtinen, M. (2011) Mate choice for optimal (k) inbreeding. *Evolution,* **65,** 1501-1505.

Ralls, K., J. D. Ballou & A. Templeton (1988) Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation biology,* **2,** 185-193.

Reeve, H. K., D. F. Westneat, W. A. Noon, P. W. Sherman & C. F. Aquadro (1990) DNA "fingerprinting" reveals high levels of inbreeding in colonies of the eusocial naked mole-rat. *Proceedings of the National Academy of Sciences,* **87,** 2496-2500.

Richardson, D. S., J. Komdeur & T. Burke (2004) Inbreeding in the Seychelles warbler: Environment-dependent maternal effects. *Evolution,* **58,** 2037-2048.

Riehl, C. & C. A. Stern (2015) How cooperatively breeding birds identify relatives and avoid incest: New insights into dispersal and kin recognition. *BioEssays,* **37,** 1303-1308.

Ross-Gillespie, A., M. J. O'Riain & L. F. Keller (2007) Viral epizootic reveals inbreeding depression in an habitually inbreeding mammal. *Evolution,* **61,** 2268-2273.

Russell, A. F., (2004) Mammals: comparisons and contrasts. In: *Ecology and Evolution of Cooperative Breeding in Birds.* W. Koenig & J. Dickinson (Eds.). Cambridge University Press, Cambridge, UK.

Russell, A. F. & B. J. Hatchwell (2001) Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proceedings of the Royal Society of London B: Biological Sciences,* **268,** 2169-2174.

Sanderson, J. L., J. Wang, E. I. Vitikainen, M. A. Cant & H. J. Nichols (2015) Banded mongooses avoid inbreeding when mating with members of the same natal group. *Molecular ecology,* **24,** 3738-3751.

Sharp, S. P., A. McGowan, M. J. Wood & B. J. Hatchwell (2005) Learned kin recognition cues in a social bird. *Nature,* **434,** 1127-1130.

Sherborne, A. L., M. D. Thom, S. Paterson, F. Jury, W. E. R. Ollier, P. Stockley, R. J. Beynon & J. L. Hurst (2007) The Genetic Basis of Inbreeding Avoidance in House Mice. *Current Biology,* **17,** 2061-2066.

Sparkman, A. M., J. R. Adams, T. D. Steury, L. P. Waits & D. L. Murray (2012) Pack social dynamics and inbreeding avoidance in the cooperatively breeding red wolf. *Behavioral Ecology,* **23,** 1186-1194.

Stoffel, M. A., M. Esser, M. Kardos, E. Humble, H. Nichols, P. David & J. I. Hoffman (2016) inbreedR: An R package for the analysis of inbreeding based on genetic markers. *Methods in Ecology and Evolution,* **7,** 1331–1339.

Szulkin, M., N. Bierne & P. David (2010) Heterozygosity-fitness correlations: a time for reappraisal. *Evolution,* **64,** 1202-1217.

Szulkin, M. & B. C. Sheldon (2008) Dispersal as a means of inbreeding avoidance in a wild bird population. *Proceedings of the Royal Society of London B: Biological Sciences,* **275,** 703-711.
Szulkin, M., K. V. Stopher, J. M. Pemberton & J. M. Reid (2013) Inbreeding avoidance, tolerance, or preference in animals? *Trends in Ecology and Evolution,* **28,** 205-211.
Tang-Martinez, Z. (2001) The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. *Behavioural Processes,* **53,** 21-40.
Thunken, T., T. C. M. Bakker, S. A. Baldauf & H. Kullmann (2007) Active inbreeding in a cichlid fish and Its adaptive significance. *Current Biology,* **17,** 225-229.
Townsend, A. K., A. B. Clark, K. J. McGowan, E. L. Buckles, A. D. Miller & I. J. Lovette (2009) Disease-mediated inbreeding depression in a large, open population of cooperative crows. *Proceedings of the Royal Society of London B: Biological Sciences,* **276,** 2057-2064.
Tregenza, T. & N. Wedell (2002) Polyandrous females avoid costs of inbreeding. *Nature,* **415,** 71-73.
van de Crommenacker, J., J. Komdeur & D. S. Richardson (2011) Assessing the cost of helping: the roles of body condition and oxidative balance in the Seychelles warbler (Acrocephalus sechellensis). *PLoS One,* **6,** e26423.
Varian-Ramos, C. W. & M. S. Webster (2012) Extrapair copulations reduce inbreeding for female red-backed fairy-wrens, Malurus melanocephalus. *Animal Behaviour,* **83,** 857-864.
Walling, C. A., J. M. Pemberton, J. D. Hadfield & L. E. B. Kruuk (2010) Comparing parentage inference software: reanalysis of a red deer pedigree. *Molecular Ecology,* **19,** 1914-1928.
Wang, C. & X. Lu (2011) Female ground tits prefer relatives as extra-pair partners: driven by kin-selection? *Molecular Ecology,* **20,** 2851-2863.
Wang, J. & A. W. Santure (2009) Parentage and sibship inference from multilocus genotype data under polygamy. *Genetics,* **181,** 1579-1594.
Waser, P. M., S. N. Austad & B. Keane (1986) When Should Animals Tolerate Inbreeding? *The American Naturalist,* **128,** 529-537.
Weisfeld, G. E., T. Czilli, K. A. Phillips, J. A. Gall & C. M. Lichtman (2003) Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *Journal of Experimental Child Psychology,* **85,** 279-295.
Wright, J., P. G. McDonald, L. te Marvelde, A. J. Kazem & C. M. Bishop (2009) Helping effort increases with relatedness in bell miners, but 'unrelated'helpers of both sexes still provide substantial care. *Proceedings of the Royal Society of London B: Biological Sciences***,** rspb20091360.
Zack, S. (1990) Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology,* **86,** 265-286.


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