ORIGINAL PAPER

Social living without kin discrimination: experimental evidence from a communally breeding bird

Christina Riehl[1] · **Meghan J. Strong**[2]

Abstract In many cooperative animal societies, individuals can recognize their relatives and preferentially direct helping behaviors towards them. However, the ability to learn kin recognition cues may be constrained in societies with low relatedness, since group membership alone is not a reliable proxy for kinship. Here, we examine kin discrimination in the greater ani (*Crotophaga major*), a communally nesting bird in which several unrelated males and females reproduce in a single, shared nest and provide parental care to the mixed clutch of young. Each adult, therefore, is closely related to some nestlings in the clutch and unrelated to others. Food is limited and starvation is a significant cause of nestling mortality, suggesting that adults should increase their fitness by preferentially feeding their own offspring in the mixed clutch. To test this hypothesis, we cross-fostered broods of nestlings between pairs of nests, such that none of the nestlings in the manipulated nests were related to any of the adults feeding them. We found no evidence that adult greater anis discriminate between their own and unrelated nestlings: adults at cross-fostered groups fed nestlings at the same rates as adults at control (sham-manipulated) nests, and rates of nestling starvation were equal at cross-fostered and control nests. These results suggest that adult greater anis do not recognize their own nestlings, and they are consistent with the hypothesis that

genetically encoded markers for kin recognition are rare in birds.

Introduction

Cooperatively breeding animals live in social groups in which several individuals provide alloparental care to a single brood of young. Because caregivers often vary in their degree of genetic relatedness to offspring in the brood, kin selection theory predicts that individuals should increase their inclusive fitness by preferentially directing care towards those to whom they are most closely related (Hamilton 1964). Many empirical studies have supported this hypothesis, finding that the ability to recognize kin is widespread in insects, mammals, and birds (reviewed in Komdeur and Hatchwell 1999; Breed 2014). In other instances, however, kin recognition is surprisingly absent, even in situations where it would be expected to confer obvious benefits (Keller 1997). Male birds, for example, are generally unable to discriminate between their own offspring and those fathered by other males, even when the risk of extra-pair paternity is high (Kempenaers and Sheldon 1996). Kin discrimination is also rare in eusocial insects: individuals typically distinguish between nestmates and non-nestmates, but not between relatives and non-relatives within the same colony (Atkinson et al. 2008; Boomsma and d'Ettore 2013).

Several hypotheses have been proposed to explain the absence of kin recognition in cooperative breeders. When group members are closely related to one another, there may be little selection pressure for the evolution of recognition

✉ Christina Riehl
  criehl@princeton.edu

1 Department of Ecology and Evolutionary Biology, Princeton University, 106A Guyot Hall, Princeton, NJ 08544, USA

2 Anthropology Department, California State University Northridge, 18111 Nordhoff St, Northridge, CA 91330, USA

mechanisms (Komdeur and Hatchwell 1999). Even when group members vary in relatedness, the evolution of such mechanisms may be constrained by the risk of errors (for example, when the costs of mistakenly rejecting one's own offspring are greater than the benefits derived from discrimination). Finally, group members may lack sufficient opportunities to learn visual, auditory, or chemical cues associated with their relatives. Although Hamilton (1964) originally proposed that kin recognition might be genetically encoded, via "recognition alleles" or phenotype matching, most empirical studies have found that kin recognition cues are instead learned through association, via indirect proxies that are likely to be correlated with kinship (Griffiths and Magurran 1999; Tang-Martinez 2001). In cooperatively breeding long-tailed tits (*Aegithalos caudatus*), for example, nestlings learn characteristic contact calls from closely related adults while they are still in the nest (Sharp et al. 2005). Adults can also learn to recognize their own young: in American coots (*Fulica americana*), adults first learn to distinguish the phenotypes of their own offspring and can subsequently discriminate against unrelated, parasitic nestlings (Shizuka and Lyon 2010). These mechanisms can only evolve when the cues are reliable—for example, when age, spatial proximity, and group membership are consistent predictors of genetic relatedness.

Instances of "true" kin recognition—the ability to recognize genetic relatives even without prior experience—have been notoriously difficult to demonstrate (Grafen 1990; Rousset and Roze 2007). However, several recent studies have re-opened the possibility of true kin recognition by showing that olfactory cues, probably encoded by genes in the major histocompatibility complex (MHC), can be used to discriminate between kin and non-kin without previous association (Todrank and Heth 2003; Krause et al. 2012; Leclaire et al. 2013). In these cases, MHC polymorphisms may provide stable signatures shared by genetically related individuals, similar to the "recognition alleles" originally envisioned by Hamilton. It is still unclear, though, whether MHC or odor-based kin recognition is widespread in social animals. Relatively few empirical studies have tested whether cooperatively breeding birds are capable of discriminating between related and unrelated nestlings, and even fewer have performed the experimental manipulations necessary to ensure that recognition is based on innate rather than learned cues (Krause et al. 2012).

Here, we ask whether the greater ani (*Crotophaga major*), a cooperatively breeding bird, is capable of kin discrimination. Anis have an unusual reproductive system that provides an ideal opportunity for testing this hypothesis: each nesting group consists of two to four genetically unrelated pairs of adults that construct a single nest in which all of the females lay their eggs. Group nesting appears to be obligate; less than 2 % of nesting units consist of lone pairs, which have never

been observed to raise young successfully (Riehl 2011). All group members, both males and females, participate in incubation, nest defense, and parental care of the shared brood of offspring. Pairs within the group are socially monogamous and predominantly genetically monogamous as well, although 10–15 % of nestlings are produced by extra-pair copulations among individuals in the same social group. Reproductive bias, or skew, is extremely low among group members, and all of the adult group members typically gain parentage in each nesting attempt (Riehl 2012). Each pair typically contributes three to four eggs to the shared clutch, and the final clutch size ranges from 6 to 15 eggs depending on the number of adults in the nesting group. Starvation is responsible for approximately 8–13 % of nestling mortality (Riehl and Jara 2009). Therefore, adult anis could theoretically increase their reproductive fitness by preferentially feeding their own offspring in the mixed clutch, since each adult is closely related to some of the nestlings and unrelated to the rest. If kin discrimination does occur, however, it must be via genetically encoded mechanisms rather than learning, since social nesting is obligate and adult breeders do not have opportunities to learn the phenotypes of their own offspring in the absence of unrelated nestlings.

In this study, we used cross-fostering experiments to determine whether adult greater anis are capable of recognizing their own nestlings in communal clutches of mixed parentage. We swapped entire clutches of nestlings between pairs of nests (controlling for nestling age, clutch size, group size, and time of year), such that all nestlings in cross-fostered nests were genetically unrelated to any of the adults feeding them. We subsequently used motion-activated nest cameras to record food deliveries to cross-fostered and control (sham-manipulated) nests, and measured (1) rates of food delivery, (2) types of prey delivered, and (3) nestling survivorship. We predicted that, if adults are capable of discriminating against unrelated nestlings, cross-fostered nests should exhibit lower rates of food delivery and higher rates of nestling starvation when compared to control nests.

Study area and methods

Study system and nest monitoring

We studied a nesting population of greater anis in the Barro Colorado Nature Monument, Panama, a 5400-ha preserve operated by the Smithsonian Tropical Research Institute. This population has been continuously monitored since 2006. Approximately 60 % of nesting units consist of two breeding pairs, 30 % of three pairs, 8 % of four or more pairs, and 2 % of lone pairs (Riehl 2011; CR 2006–2014 unpubl. data). Approximately 15–20 % of nesting groups also contain at least one unpaired "helper," typically a non-breeding male

from a previous nesting attempt that has delayed dispersal (Riehl and Jara 2009). For this study, we did not include groups that contained non-breeding helpers so as to restrict the experiments to nesting groups where all of the adult group members were reproductive. The habitat at this study site is tropical lowland forest bordering Gatún Lake; anis build large, open-cup stick nests along the water's edge, in tree branches overhanging the water or in emergent vegetation close to the shoreline (Riehl and Jara 2009). Nesting is restricted to the rainy season, typically late June–late September. Groups remain on nesting territories year-round and typically re-use the same nest site for many years, although foraging and roosting areas are overlapping during the non-breeding season. Incubation requires 11–12 days and nestlings typically remain in the nest for 2–3 weeks before fledging, although nestlings are capable of climbing out of the nest, swimming, and hiding in surrounding vegetation as early as 5 days after hatching. Nestlings are fed primarily on large insects (Orthoptera, Mantodea, Blattodea), spiders, and small vertebrates (including young green iguanas, *Iguana iguana*, and *Ameiva* spp.) Young anis stay with their natal group for approx. 8 months after fledging; approx. 85 % of offspring then disperse and the remainder stay with their natal groups as non-breeding helpers for up to 2 years (Riehl and Jara 2009; Riehl 2011).

All nests were located and checked by boat (details in Riehl and Jara 2009). Nests were checked daily during the laying period, every 3–4 days during incubation, and daily during the nestling period. As part of long-term data collection, eggs were numbered sequentially with a non-toxic marker in the order in which they were laid and the fate of each egg was recorded. Nestlings were banded with a unique combination of colored leg bands at 4–5 days of age, and a small blood sample (>10 μL) was taken from the ulnar vein for genetic analyses (details in Riehl 2011).

Experimental design

We conducted reciprocal cross-fostering experiments at five pairs of nests in order to test whether adult anis are capable of recognizing their own nestlings in communal clutches. Each pair of nests was matched for group size (two to three pairs/group), clutch size (three to seven nestlings/clutch), and age of nestlings (1–3 days). Due to the difficulty of identifying appropriately matched nests that were in relatively close proximity, two pairs of nests were cross-fostered in 2008, two pairs in 2009, and one pair in 2012. All nestlings in the clutch were swapped with the nestlings in the paired nest, ensuring that none of the cross-fostered nestlings remained in their original nest. Extra-pair copulations do occur in this study population, but previous analyses showed that extra-pair copulations outside the nesting group are rare (~3 % of nestlings; Riehl 2012). Therefore, it is extremely unlikely that any of the adults tending experimental nests were genetic parents of any of

the foster nestlings. Exchanges took less than 20 min to perform.

For 2–4 days following cross-fostering, we measured food delivery rates and nestling survivorship at cross-fostered nests, and compared these values with those measured at sham-manipulated control nests. After a maximum of 4 days, nestlings were returned to their original nests and subsequently raised by the adults in their natal group. For each pair of manipulated nests, two control nests were randomly chosen from the study population that matched the manipulated nest for year, group size, clutch size, and age of nestlings. Nestlings at control nests were removed for 20 min and then returned to the original nest. The cross-fostering period was only 2–4 days at each nest since nestlings develop extremely rapidly and will fledge prematurely if they are disturbed after 6 days post-hatching. Nests were checked every 1–2 days until the nestlings fledged or died, in order to record rates of starvation, depredation, and nest success.

Rates of food delivery were recorded for at least 12 h per nest over the 2–4 days following cross-fostering, using digital motion-activated nest cameras (Wingscapes BirdCams, Alabaster, AL, USA). These cameras use infrared sensors to detect changes in motion and temperature; photographs were stored on 32-gig SDHC memory cards and stamped with the time and date of the photograph. In order to collect at least 12 h of data per nest, total observation periods varied from 2 to 4 days across nests due to weather (rain events), limits on camera battery life, and logistics. Details of camera placement and protocols followed Riehl and Jara (2009). A pilot test in which a human observer simultaneously recorded food deliveries to nests indicated that cameras captured only ~90 % of food deliveries, since some visits were too rapid to be fully captured by the camera (CR unpubl. data 2008). However, since the same camera protocols were used at all nests, this should not have biased the comparisons between control and cross-fostered nests.

Statistical analysis

We recorded a total of 308 h of footage at 20 different nests (five pairs of cross-fostered nests and ten control nests). Two of these 20 nests were excluded from the final analysis because they were depredated during the recording period. Statistical analysis of camera footage showed that adults typically returned to the nest and resumed normal rates of food delivery within 15 min of an observer's visit to the nest (data not shown); therefore, at each nest, the first 20 min of footage following any observer's visit to the nest was excluded from analysis. In addition, periods of poor weather (rain and low-light conditions) were also excluded from the analysis, because the presence of rain affected both food delivery rate and camera sensitivity. Following these exclusions, we

analyzed a total of 262 h of footage at 18 nests (mean=14.5 h per nest±SD=3.0; range=12–21 h per nest).

Provisioning rates were calculated as the number of food deliveries per hour per adult group member. Since we could not identify individual adults in all of the nesting groups, the provisioning rate is therefore an average measure of the overall frequency of food deliveries to the nest, corrected by group size. We first used matched-pair t tests to directly compare the provisioning rates at cross-fostered nests vs. control nests, since the experimental design controlled for clutch size, group size, and nestling age. In order to identify other factors predicting variation in provisioning rate, we then performed a more general analysis by pooling the data from all nests and constructing generalized linear models in STATA. Since the response variable was a rate (food deliveries/hour/individual) and the data followed a Poisson distribution, we used a Poisson response distribution and a logarithmic link function in the models. Predictor variables included group size (four or six adults), clutch size (three to eight nestlings), nestling age (1–4 days), and experimental treatment (cross-fostered or control). The variance in the response variable was not larger than the mean, so we did not correct for overdispersion.

We constructed a second logistic regression to identify factors influencing the probability of starvation occurring at a nest. Since the response variable was binary (starvation vs. no starvation), we used a binomial error structure and a logit link function. The predictor variables used were identical to those in the first set of models. For both response variables (food delivery rate and starvation), initial models included all predictor variables and two-way interactions between experimental treatment and group size, clutch size, and nestling age. Final models were chosen by comparison of AICc among all possible models, rather than by stepwise elimination of variables (Burnham and Anderson 2002).

Results

Rates of food delivery to nestlings

Rates of food delivery to nestling greater anis did not differ between control and cross-fostered nests (control mean=1.35 deliveries/h/adult±SE=0.12; cross-fostered mean=1.39± 0.17; matched-pairs $t=-0.27$, df=7, two-tailed $P=0.8$; Fig. 1). Consistent with this result, the best-fit generalized linear model identified clutch size and group size as significant predictors of food delivery rate but not experimental treatment or nestling age (Table 1). Parameter values from the model revealed that per capita food delivery rates decreased with group size (the number of adults delivering food to the clutch) and increased with clutch size (the number of nestlings receiving food). When the total delivery rate was modeled as the response variable instead of per capita delivery rate, clutch size was the only significant predictor ($P=0.02$; full model results not shown). Therefore, adult greater anis increased their food delivery rate in response to larger clutches; however, controlling for clutch size, nests with more attending adults did not experience higher overall rates of food delivery ($P>0.1$). There were no significant interactions between experimental treatment and any of the predictor variables ($P>0.05$).

Probability of starvation

The probability of starvation for nestling greater anis did not differ between control and cross-fostered nests (control, 4 of 43 nestlings died of starvation [9.3 %]; cross-fostered, 4 of 51 [7.8 %]; Fisher's exact test, $P=1.0$; Fig. 1). Starvation occurred at 6 of the 18 nests under observation; 1 nestling starved in each of 4 clutches and 2 nestlings starved in each of 2 clutches. The average number of nestlings in clutches where starvation occurred was significantly larger than in clutches where starvation did not occur (nests with starvation: clutch size mean=7.0±SD=0.89; nests without starvation: mean=5.08±1.68, unequal-variance $t_{16}=3.16$, $P=0.006$). The sample size (18 nests) was too small for a full model including all possible predictors to converge; however, a simpler logistic regression confirmed that clutch size was a significant predictor of starvation, with starvation more likely to occur in nests with large clutches (>5 nestlings) than small clutches (≤5 nestlings; $z=24.1$, $P=0.03$). Experimental treatment did not have a significant effect ($z=0.94$, $P=0.35$).

Discussion

The communal nesting system of greater anis is unusual: several unrelated pairs of adults share breeding within a single nest, such that each adult in the group is the genetic parent of some of the nestlings in the mixed clutch, but unrelated to the rest. In this study, we found no evidence that adult anis are capable of recognizing and preferentially feeding their own nestlings. Food delivery rates and nestling survivorship were statistically indistinguishable between control nests and cross-fostered nests, in which none of the adults attending the nest were related to any of the nestlings that they fed. Other anecdotal observations support the hypothesis that adult greater anis care for nestlings indiscriminately, regardless of kin relationships. For example, in one clutch in which all but one nestling died, all six adult group members continued to defend and feed the lone survivor, even though microsatellite analysis confirmed that the nestling was related to only two of the adults (CR, pers. obs. 2008). Similarly, although adult group members have been observed to divide the brood after fledging and feed different offspring, brood division in at least two

Fig. 1 Mean food delivery rate (*black bar*, *left axis*) and percentage of nestlings that died of starvation (*white bar*, *right axis*) at greater ani nests under control or cross-fostered experimental treatments. *Error bars* indicate ±standard error and ±90 % confidence interval, respectively
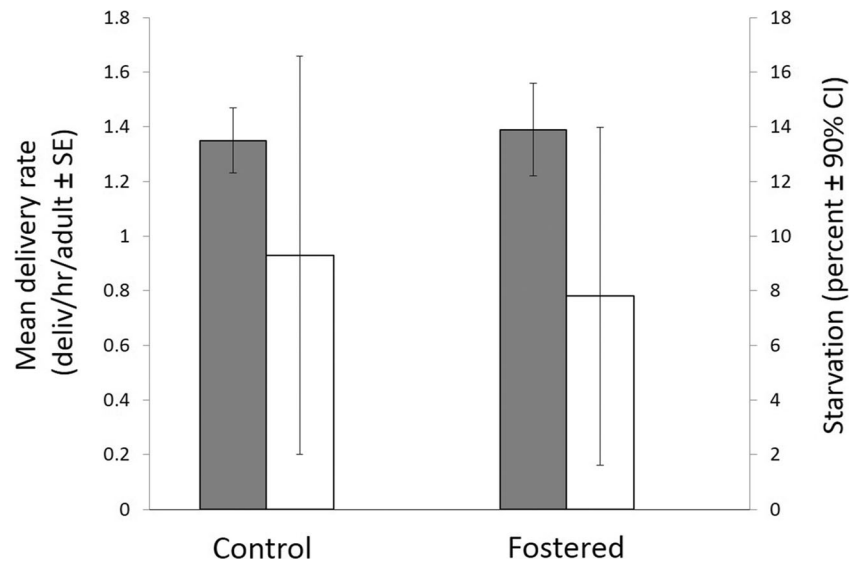
cases did not parallel genetic relationships (CR and L. Jara, pers. obs. 2007–2008).

The apparent inability of greater anis to recognize their own offspring is puzzling, given the sophisticated kin discrimination mechanisms that have been described in some other animals. However, it is important to recognize that the inability to recognize nestlings is probably ancestral in birds: recognition appears to have evolved only in a few species and under very restricted circumstances (Beecher 1988). Kempenaers and Sheldon (1996) outlined two hypotheses that may explain the absence of kin discrimination by adult birds: (1) adults do not discriminate against unrelated nestlings because there are no fitness benefits to be gained by doing so or (2) offspring recognition is adaptive, but adults are incapable of it because there are no reliable "rules of thumb" for recognizing kin, and genetically encoded cues or labels do not exist.

Given that the risk of starvation for ani nestlings is not zero, it would seem obviously adaptive for adults to recognize their offspring and preferentially feed them. However, it is likely

that the low variation in reproductive fitness among adults in ani groups has led to reduced selection for the ability to recognize their kin. Unlike most cooperatively breeding birds, all adult anis in a group typically breed in each reproductive attempt, and the division of reproduction among group members is roughly egalitarian (Riehl 2011). All group members, therefore, have an approximately equal probability of being the genetic parent of a given nestling in the clutch, and the costs of delivering food to an unrelated nestling are essentially compensated for by the other group members. As a result, variation in reproductive fitness among individuals within ani groups is relatively low compared to the variation in fitness between groups (Riehl 2012). Nevertheless, this argument does not imply that there is no selection on adults to recognize their own nestlings, since those that could do so could still, on average, increase their reproductive output relative to those that could not.

Beecher (1988) proposed a complementary adaptive hypothesis for the absence of nestling recognition in birds, based on the fitness perspective of the nestling rather than the adult. He suggested that, in situations where parentage is uncertain, nestlings should generally benefit from concealing their kinship ties rather than advertising them. Selection should not favor nestlings that signal their genetic identity, since, if unrelated to the provisioning adult, those nestlings would suffer from an increased risk of starvation or infanticide. Furthermore, the strength of selection on nestlings to hide their genetic identity should increase as the frequency of mixed parentage increases, thereby opposing the increased selection on adults to develop the ability to discriminate (Kempenaers and Sheldon 1996). Since both starvation and infanticide have been documented in anis (Riehl and Jara 2009; Quinn et al. 2010), the inability of greater anis to recognize their own nestlings may reflect an evolutionary conflict of interests

Table 1 Final generalized linear model testing the effects of clutch size, group size, nestling age, and experimental treatment (cross-fostered vs. control) on the average rate of food delivery to greater ani nests (deliveries per hour per adult)

Parameter	Coefficient	Std. error	z	$P>|z|$
Intercept	1.07	0.41	0.56	——
Clutch size	0.69	0.15	2.84	*0.005*
Group size	−0.38	0.17	−2.01	*0.05*
Nestling age	0.21	0.48	0.48	0.63
Treatment	−0.25	0.37	−0.66	0.51

Significant effects are in italics

between the signalers (nestlings) and the receivers (their caregivers).

Alternatively, the acquisition of kin recognition cues in greater anis may be constrained by their complex social system. For most birds, the nestling's physical association with the nest is itself a reliable proxy for genetic relatedness, and parents have a window of time to learn offspring phenotypes. In colonially nesting seabirds, for example, parents typically learn to identify the vocalizations of their nestlings in the first few days after hatching, and subsequently use those vocalizations to locate their offspring after fledging (reviewed in Insley et al. 2003). Learned recognition cues appear to have evolved in several other contexts in birds, including in cooperative breeders that nest with close kin (Payne et al. 1988; Price 1999; Komdeur et al. 2004; Sharp et al. 2005; Shizuka and Lyon 2010).

In more complex societies like that of the greater ani, where kin and non-kin are regularly raised in the same nest, kin recognition cues must be genetically inherited since individuals do not have such opportunities. To our knowledge, the only study that has demonstrated the existence of genetically encoded recognition cues in a cooperatively breeding vertebrate is that of McDonald and Wright (2011), who found that bell miners (*Manorina melanophrys*) use inflexible, innate vocalizations to distinguish kin in large coteries composed of both relatives and non-relatives. Learning-based mechanisms to recognize kin appear to be more frequent than genetically encoded cues, at least in birds. Understanding the factors that constrain the evolution of offspring recognition—including phylogenetic inertia, parent-offspring conflict, the high cost of recognition errors, and the evolutionary instability of phenotypic recognition cues—may help explain several puzzling avian phenomena, including the near-universal acceptance of extra-pair young by cuckolded males and the frequent inability of hosts to reject brood-parasitic nestlings.

Ethical standards All experimental manipulations in this study were approved by the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (STRI, protocol number 2007-02-03-15-07) with the authorization of Panama's Autoridad Nacional del Ambiente (ANAM).

Conflict of interest The authors declare that they have no competing interests.

References

Atkinson L, Teschendorf G, Adams ES (2008) Lack of evidence for nepotism by workers tending queens of the polygynous termite *Nasutitermes corniger*. Behav Ecol Sociobiol 62:805–812

Beecher MD (1988) Kin recognition in birds. Behav Genet 18:465–482

Boomsma JJ, d'Ettore P (2013) Nice to kin and nasty to non-kin: revisiting Hamilton's early insights on eusociality. Biol Lett 9:20130444

Breed M (2014) Kin and nestmate recognition: the influence of W. D. Hamilton on 50 years of research. Anim Behav 92:271–279

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York

Grafen A (1990) Do animals really recognize kin? Anim Behav 39:42–54

Griffiths SW, Magurran AE (1999) Schooling decisions in guppies (*Poecilia reticulata*) are based on familiarity rather than kin discrimination by phenotype matching. Behav Ecol Sociobiol 45:437–443

Hamilton WD (1964) The genetical evolution of social behaviour. II. J Theor Biol 7:17–52

Insley SJ, Paredes R, Jones IL (2003) Sex differences in razorbill *Alca torda* parent-offspring vocal recognition. J Exp Biol 206:25–31

Keller L (1997) Indiscriminate altruism: unduly nice parents and siblings. Trends Ecol Evol 12:99–103

Kempenaers B, Sheldon BC (1996) Why do male birds not discriminate between their own and extra-pair offspring? Anim Behav 51:1165–1173

Komdeur J, Hatchwell BJ (1999) Kin recognition: function and mechanism in avian societies. Trends Ecol Evol 14:237–241

Komdeur J, Richardson DS, Burke T (2004) Experimental evidence that kin discrimination in the Seychelles warbler is based on association and not genetic relatedness. Proc R Soc Lond B 271:963–969

Krause ET, Krüger O, Kohlmeier P, Caspers BA (2012) Olfactory kin recognition in a songbird. Biol Lett 8:327–329

Leclaire S, Nielsen JF, Thavarajah NK, Manser M, Clutton-Brock TH (2013) Odour-based kin discrimination in the cooperatively breeding meerkat. Biol Lett 9:20121054

McDonald PG, Wright J (2011) Bell miner provisioning calls are more similar among relatives and are used by helpers at the nest to bias their effort towards kin. Proc R Soc Lond B 278:3403–3411

Payne RB, Payne LL, Rowley I (1988) Kin and social relationships in fairy-wrens: recognition by song in a cooperative bird. Anim Behav 36:1341–1351

Price JJ (1999) Recognition of family-specific calls in stripe-backed wrens. Anim Behav 57:483–492

Quinn JS, Samuelsen A, Barclay M, Schmaltz G, Kahn H (2010) Circumstantial evidence for infanticide of chicks of the communal smooth-billed ani (*Crotophaga ani*). Wilson J Ornithol 122:369–374

Riehl C (2011) Living with strangers: direct benefits favour non-kin cooperation in a communally nesting bird. Proc R Soc Lond B 278:1728–1735

Riehl C (2012) Mating system and reproductive skew in a communally breeding cuckoo: hard-working males do not sire more young. Anim Behav 84:707–714

Riehl C, Jara L (2009) Natural history and reproductive biology of the greater ani (*Crotophaga major*) at Gatún Lake, Panama. Wilson J Ornithol 121:678–687

Rousset F, Roze D (2007) Constraints on the origin and maintenance of genetic kin recognition. Evolution 61:2320–2330

Sharp SP, McGowan A, Wood MJ, Hatchwell BJ (2005) Learned kin recognition cues in a social bird. Nature 434:1127–1130

Shizuka D, Lyon BE (2010) Coots use hatch order to recognize and reject conspecific brood parasitic chicks. Nature 463:223–228

Tang-Martinez Z (2001) The mechanisms of kin discrimination and the evolution of kin recognition in vertebrates: a critical re-evaluation. Behav Process 53:21–40

Todrank J, Heth G (2003) Odor-genes covariance and genetic relatedness assessments: rethinking odor-based "recognition" mechanisms in rodents. Adv Stud Behav 32:77–130