

Extrapair Copulations Predict Extrapair Fertilizations in the American Crow

Author: Townsend, Andrea K.

Source: The Condor, 111(2) : 387-392

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/cond.2009.090010>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

The Condor 111(2):387–392
 © The Cooper Ornithological Society 2009

EXTRAPAIR COPULATIONS PREDICT EXTRAPAIR FERTILIZATIONS IN THE AMERICAN CROW

ANDREA K. TOWNSEND¹

Fuller Evolutionary Biology Program, Cornell University Laboratory of Ornithology, Ithaca, NY 14850

Abstract. The general relationship between extrapair copulations (EPC) and extrapair paternity (EPP) in wild birds is unclear because relatively few studies have collected both types of information from a single population. I compared observed copulatory behavior with genetic paternity in a population of the American Crow (*Corvus brachyrhynchos*). For each group of nesting crows, the proportion of extrapair young in a brood was higher when EPC attempts were observed in the group that year. The overall proportion of broods with extrapair young was identical to the proportion of focal group-years in which EPC attempts were observed (32%). In a given brood, however, observed EPC attempts did not always predict EPP, and failure to observe EPCs

did not always predict monogamy. Furthermore, males observed attempting EPCs often differed from the males gaining EPP, suggesting that EPCs were attempted by multiple males with certain females in certain years. Observed EPC attempts were initiated by males, and most appeared to be resisted by females.

Key words: *American Crow, Corvus brachyrhynchos, extrapair paternity, extrapair copulation, forced copulation.*

Las Copulaciones Extra-Pareja Predicen las Fertilizaciones Extra-Pareja en *Corvus brachyrhynchos*

Resumen. En las aves silvestres, la relación general entre las copulaciones extra-pareja (CEP) y la paternidad extra-pareja (PEP) no es clara debido a que relativamente pocos estudios han colectado los dos tipos de información de una misma población. Comparé el comportamiento de cópula observado con datos de

Manuscript received 12 January 2009; accepted 26 March 2009.

¹E-mail: at256@cornell.edu

The Condor, Vol. 111, Number 2, pages 387–392. ISSN 0010-5422, electronic ISSN 1938-5422. © 2009 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, <http://www.ucpressjournals.com/reprintInfo.asp>. DOI: 10.1525/cond.2009.090010

paternidad genética en una población de *Corvus brachyrhynchos*. La proporción de juveniles engendrados fuera de la pareja en una nidada fue más alta cuando se observaron intentos de CEP en el grupo durante ese año. La proporción general de nidadas con juveniles engendrados fuera de la pareja fue idéntica a la proporción de grupos focales de un año en que se observaron intentos de CEP (32%). Sin embargo, en una nidada determinada, los intentos de CEP observados no siempre predijeron la PEP, y la ausencia de observaciones de intentos de CEP no siempre predijo monogamia. Además, los machos observados en intentos de CEP generalmente difirieron de los machos que ganaron PEP, lo que sugiere que varios machos intentaron CEP con ciertas hembras en ciertos años. Los intentos de CEP observados fueron iniciados siempre por los machos y la mayoría de los intentos parecieron ser rechazados por las hembras.

Few socially monogamous species of birds are genetically monogamous (Griffith et al. 2002). For males, extrapair paternity (EPP) provides an opportunity to sire offspring, for which they usually provide little parental care, outside of their social pair bonds. For females, EPP might provide an opportunity to acquire genetic or direct benefits from extrapair males (Jennions and Petrie 2000, Griffith et al. 2002), and the majority of current research has focused on the potential adaptive benefits of EPP for females (Griffith et al. 2002). Although in some species there is evidence suggesting that females might seek their extrapair partners (Neudorf et al. 1997, Double and Cockburn 2000, Pedersen et al. 2006), relatively few extrapair copulations (EPCs) have actually been documented, and some of these appear to be unsolicited, or even resisted, by females (reviewed in Westneat and Stewart 2003). Across taxa, evidence for genetic benefits of EPP derived by females is mixed (Akçay and Roughgarden 2007, Kempenaers 2007, Mays et al. 2008), and in general the degree to which we might expect EPP to be sought by females for its fitness benefits is debatable (Arnqvist and Kirkpatrick 2005, 2007, Griffith 2007). Available data appear insufficient to resolve the issue (Eliassen and Kokko 2008).

If EPP is generally male-driven in a given system, extrapair fertilizations could occur in two ways. First, extrapair males might coerce unwilling females to copulate, although the ability of males without intromittent organs to force females to copulate is controversial (Gowaty and Buschhaus 1998, Westneat and Stewart 2003). Alternatively, females might submit to EPCs with some extrapair males to reduce the cost of harassment (Westneat and Stewart 2003, Arnqvist and Kirkpatrick 2007). In general, females would be expected to submit to EPCs when the costs of resisting exceed the costs of submitting (Eliassen and Kokko 2008). Even if some males do successfully copulate with unwilling females, however, females might be able to exercise post-copulatory choice over the success of the fertilization (Birkhead and Moller 1992, Gowaty and Buschhaus 1998). For example, given the potential costs of inbreeding depression (Keller and Waller 2002, Townsend et al. 2009a), a female that is coerced into copulation with a closely related male might attempt to decrease the probability of successful fertilization (e.g., through sperm ejection; Birkhead and Moller 1992, page 82). Males are, however, likely to coevolve mechanisms to increase their probability of successful fertilizations (Westneat and Stewart 2003).

Many recent studies of the evolution of EPCs have focused entirely on genetic patterns of EPP, without corresponding information of how this paternity relates to copulatory behavior itself (Griffith 2007), and without information on whether in a given population males or females generally appear to seek EPCs (Westneat and Stewart 2003). Multispecies reviews have

suggested that the frequency of observed EPC might have little or no predictive power about the level of EPP, and that the relationship between the two is indirect (Dunn and Lifjeld 1994, Birkhead and Moller 1995). Griffith (2007) suggested that the nature of the relationship between EPC and EPP is critical to understanding their functions, and that the following questions should be addressed empirically: What is the proportion of females in a given population involved in EPCs? How does this proportion relate to the proportion of broods with EPP? What is the variation among females in extrapair behavior, and how does this variation relate to actual EPP?

I examined the relationship between observed EPC attempts and realized EPP in the cooperatively breeding American Crow (*Corvus brachyrhynchos*). Within-pair and extrapair copulatory behaviors have been described from New York and Florida (Kilham 1984, Townsend et al. 2009b). Although some of the American Crows in the New York population that attempted EPCs achieved paternity (Townsend et al. 2009b), the general relationship between observed EPC attempts and the occurrence of EPP in these crows is unclear. In this population, the costs of inbreeding depression are high: the probability of survival is lower and the probability of disease is higher among offspring produced by first- and second-order kin pairs than among offspring whose parents are less related (Townsend et al. 2009a). Here, I address the following four questions: (1) Do observations of EPC attempts predict the proportion of extrapair young in a given brood? (2) Does the proportion of group-years in which EPC attempts are observed correspond to the proportion of broods in the population containing extrapair young? (3) Are the individual males observed attempting EPCs always the same males that achieve paternity? (4) Does relatedness of these prospective extrapair males to the breeding female influence the males' probability of paternity?

METHODS

STUDY AREA AND FIELD OBSERVATION

From 2005 to 2008, I examined mating behavior and genetic parentage in a suburban population of American Crows in Ithaca, New York, that has been monitored continuously since 1989 (McGowan 2001, Clark et al. 2006). In this population, family groups consist of a behaviorally distinct socially monogamous pair, assisted at the nest by 0–10 auxiliaries of either sex (mean group size 2004–2007 = 4 ± 0.22 birds, range 2–9 birds). Although these auxiliaries are often adult or subadult offspring from previous broods, some are adult males unrelated to the breeding female: stepsons, nondescendent kin of the male breeder, or completely unrelated birds, as described by Townsend et al. (2009b). Most birds belonging to focal family groups were banded or identifiable by unique scars. During most breeding attempts, there was not more than one unmarked individual in each group (range 0–2).

I monitored groups from February to July (2–7 days per week) to document group membership and social role, mate guarding, within-pair and extrapair copulations, incubation, hatching, and fledging. From August to January, I observed each group at least once per month to record membership and interactions among members. In 2007 and 2008, I made focal observations of family groups during the nest-building, egg-laying, and early incubation periods (ending observations by the second day of incubation). I recorded all within-pair and extrapair copulation attempts during one to four focal observations per family group (25–150 min per focal observation, depending on how long

a family group could be followed on a given day). All members of focal families were tightly associated with the breeding female on their respective territories in this early breeding period. Group activities were conspicuously centered around prospective nest trees in open habitat (e.g., yards, cemeteries, and golf courses) and therefore were easy to monitor. Each day, observation periods began when the breeding female of a group was first located. Observation periods ended either after a predetermined interval or sooner, if the female of the group (generally closely accompanied by her pair male and other group members) disappeared from my line of sight behind a structure in her territory, such as a house, or if the group flew out of my sight (usually as a cohesive unit) while chasing aerial predators or conspecific intruders. Females were therefore visible throughout the duration of the focal observations.

GENETIC SAMPLING AND ANALYSES

On days 24–30 after hatching, my collaborators climbed to each nest to mark nestlings with unique combinations of metal bands, color bands, and patagial tags. We collected blood (~150 μ L) from the brachial vein of live nestlings and tissue samples from dead nestlings in and under these nests. I extracted DNA from 124 of the 125 marked and unmarked adult birds in these groups, using blood sampled from these individuals as nestlings, or passively molted feathers collected while the adults were provisioning nestlings or fledglings on their territories (June–August). I regentyped unmarked birds present over multiple years with new feathers collected each year to reconfirm their identity. One auxiliary present only in a single year disappeared before it could be sampled. I extracted DNA from blood samples by using Perfect gDNA Blood Mini kits (Eppendorf, Westbury, NY) and from feather tips by using DNeasy tissue kits (Qiagen, Valencia, CA). I genotyped offspring and family members at 10 polymorphic microsatellite loci (Tarr and Fleischer 1998, Schoenle et al. 2007), and I used the maximum-likelihood approach for parentage analyses in the program CERVUS 3.0 (Kalinowski 2007), following Townsend et al. (2009b). Following methods described by Townsend et al. (2009a), I used genetic and pedigree data to assess relatedness among group members and between breeding pairs. I used the program KINGROUP (Konovalov et al. 2004) to estimate coefficients of relatedness between all dyads of female with their pair males and with their prospective extrapair sires.

STATISTICAL ANALYSES

To examine the relationship between observed EPC attempts and EPP, I analyzed the proportion of offspring produced by extrapair males in a given brood as a function of observed EPC attempts (yes/no) in a generalized linear model (GLM) with binomial errors and logit link function, weighted by the total number of offspring in the brood, in R version 2.7.2 (R Development Core Team, 2008), using the broods for which I had corresponding focal observations in that group-year ($n = 25$ broods). There was no evidence of overdispersion in the data. One assumption of this model was that my likelihood of observing EPCs was not dependent on the time I spent watching a given group. This assumption appeared to be valid: in a one-tailed two-sample t -test, the mean number of observation-minutes for group-years in which I observed EPCs (226.6 ± 38.5 min, $n = 8$ group-years) was not significantly higher than the mean number of observation-minutes for the other group-years (194.5 ± 31.4 min, $n = 17$ group-years; $t_{23} = -0.6$; $P = 0.28$). The values reported are means \pm SE.

TABLE 1. Observed EPC attempts, occurrence of EPP, and number and identity of males observed attempting EPCs. The male's relationship to the breeding female (when known) indicated by superscripts. Additional details provided in text.

Group	Number of auxiliaries observed attempting EPCs	Number of auxiliaries attaining EPP	EPCs by extragroup males observed?	EPP by extragroup males?
1	1 ^a	1	No	No
2	1 ^b	1	No	No
3	3 ^a	1	No	No
4	1 ^b	1 ^c	No	No
5	1 ^c	0	No	Yes
6	0	1 ^c	Yes	No
7	1 ^b	0	Yes	No
8	0	0	Yes	Yes
9	0	0	Yes	No

^aStepson; unrelated to the breeding female.

^bNon-descendent kin of the breeding male; unrelated to the breeding female.

^cSons; first-order kin of the breeding female.

To examine whether the probability of paternity varied with relatedness of prospective extrapair males to the breeding female, I analyzed paternity (yes/no) of a given prospective extrapair sire as the response in a generalized linear mixed model (GLMM), with coefficients of relatedness between dyads of prospective extrapair sires and females as the predictor. I specified binomial errors and family as random effects and used the penalized quasi-likelihood method. I included in this analysis all genotyped males that were known to have attempted EPCs, including both those observed attempting EPCs ($n = 9$ males; Table 1) and those that achieved EPP but were not observed attempting EPCs ($n = 7$ males). Similarly, to see if a prospective extrapair male was more likely to achieve paternity when he was less related to a female than she was to her social mate, I examined paternity (yes/no) as the response in a GLMM with the difference between relatedness coefficients (i.e., the coefficient of the social pair minus the coefficient of the female–extrapair male dyad) as the predictor, again specifying binomial errors and family as random effects.

RESULTS

I analyzed genetic paternity data from 71 broods from 25 family groups: 18 broods in 2005, 21 in 2006, 19 in 2007, and 13 in 2008. The number of analyzed broods varied annually because some nests failed before offspring were sampled. For 25 of these broods, I recorded corresponding focal observations of copulatory activity in their respective family between 17 March and 7 April 2007 and between 14 March and 5 April 2008. I made 85 focal observations for a total of 99.6 hr (mean number of observation minutes = 70.31 ± 3.13 per focal observation), with a mean of 2.65 ± 0.2 focal observations per group-year. During the other 46 group-years, I observed and recorded copulatory behavior incidentally during nest building, egg laying, and early incubation.

In the course of both the focal observations and incidental observations, I observed six within-pair copulations and 15 EPC attempts. Details of all within-pair copulations and 14 of these EPC attempts were given by Townsend et al. (2009b). Prior to each within-pair copulation, the male approached the female from the front and she performed precopulatory displays (described

by Kilham 1984), lowering herself to the ground and quivering her wings. All within-pair copulations appeared successful. In contrast, all of the EPC attempts observed from 2005 to 2007 appeared to be unsolicited by, and vigorously resisted by, breeding females: females did not perform precopulatory displays prior to these copulation attempts and appeared to resist them by flapping their wings throughout and vocalizing loudly. All attempted EPCs were interrupted by the breeding male, and none appeared to be successfully completed. An additional EPC attempt observed in 2008 resembled those described by Townsend et al. (2009b) in that it appeared to be unsolicited by the breeding female, was not prefaced with precopulatory displays, and was quickly interrupted by the breeding male. It differed from previous observations of EPC attempts in that the female did not appear to resist: she lowered herself to the ground and did not appear to struggle. I did not observe females from other territories enter my focal territories and/or solicit EPCs from any of my focal males.

Attempted EPCs were observed in 9 of the 25 family groups (36%), in 9 of 71 of group-years (13%). Most EPC attempts were recorded during the focal observations and involved eight of 21 family groups (38%) in 25 group-years (32%). Of 252 genotyped offspring, 49 were sired by extrapair males (19%), distributed in 23 of 71 broods (32%). Twenty-three extrapair offspring (9%) were sired by auxiliary males from within the group, and 26 (10%) were sired by extragroup males. Among the 25 broods for which I had corresponding focal observations, there was a higher proportion of extrapair young when EPC attempts had been observed in the early breeding season of that group-year (GLM, $1.2 \pm 0.3\%$, $\chi^2_1 = 18.7$, $P < 0.001$; Figure 1), although the males that actually gained EPP often differed than the males observed attempting EPCs (Table 1). Success of prospective extrapair males did not vary with their relatedness to the breeding female (GLMM, 0.6 ± 13.5 , $t_5 = 0.4$, $P = 0.97$), and prospective sires were not more successful when they were less related to the female than she was to her social mate (GLMM, -1.1 ± 2.1 , $t_5 = -0.5$, $P = 0.6$).

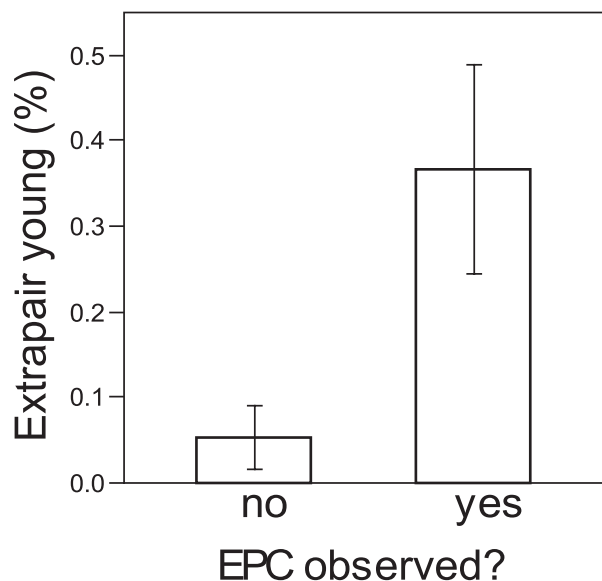


FIGURE 1. Mean proportion of extrapair offspring per brood (\pm SE) in relationship to EPC attempts observed in that group-year ($n = 25$ groups for which focal observations were conducted).

Success of individual males attempting EPCs and their kinship to the breeding male and female are summarized in Table 1. In groups 1 and 2, auxiliary males were observed repeatedly attempting EPCs with the resisting females, and they successfully attained paternity in the brood. In group 3, three auxiliary males repeatedly attempted to mount the resisting female simultaneously, but only one of these auxiliaries attained paternity. In group 4, an EPC attempt was observed by an auxiliary that the female did not appear to resist, but this auxiliary did not achieve paternity; another auxiliary did achieve paternity within that brood, however, even though he was never observed attempting EPCs. In group 5, repeated EPC attempts were made by a within-group auxiliary male with the resisting female, but EPP was achieved only by extragroup male(s). Conversely, in group 6, an EPC attempt was observed by an extragroup male on a resisting female, but EPP was instead due to a within-group auxiliary. In group 7, EPCs were attempted by both a within-group auxiliary and an extragroup male, but there were no extrapair offspring in the brood. In group 8, a single extragroup male was observed attempting an EPC with an incubating female, and there were offspring sired by extragroup male(s) in her brood. In group 9, six extragroup males attempted simultaneously to mount an incubating female, but there were no extrapair young in her brood.

DISCUSSION

In this population, the proportion of extrapair young in a given brood was higher when EPC attempts were observed in the early breeding season of the associated group-year. In the 25 group-years for which I had focal observations in the early breeding season, the proportion of group-years in which EPC attempts were observed (32%) mirrored the overall proportion of broods in the population that contained extrapair young (32%). However, observed EPC attempts did not always predict EPP in a given brood, and failure to observe EPCs did not always predict monogamy: in two of the 25 focal group-years, there were no extrapair offspring in broods for which EPC attempts were observed, and in two other group-years, there were extrapair young in focal broods for which no EPCs were observed.

One key assumption of many studies of the evolution of EPC is that patterns of genetic paternity reflect patterns of a given female's copulatory behavior (Arnqvist and Kirkpatrick 2005, Griffith 2007), even though the relationship between observed EPCs and the overall level of EPP within populations and across species appears generally weak and nonlinear (Dunn and Lifjeld 1994, Birkhead and Moller 1995). In the American Crow, the observed frequency of attempted EPCs did indeed appear higher among females with a higher proportion of extrapair young in their broods, although the relationship between observed EPC attempts and EPP was far from simple. Individual males that I observed attempting EPCs were not necessarily those that attained paternity in a given brood, suggesting that a female involved in one observed EPC attempt was likely to be involved in other EPC attempts with other males in a given year.

Another assumption frequent in the literature is that it is generally the female that seeks EPCs (Westneat and Stewart 2003, Griffith 2007), and therefore females with more extrapair young in their broods are more promiscuous. As discussed elsewhere (Townsend et al. 2009b), my data do not support the idea that females sought observed EPCs: out of 15 observed EPC attempts, only one was not vigorously resisted by the female breeder. Males, not females, initiated these EPC attempts. All attempted EPCs observed occurred on the females' territories. I did not observe focal females foraging into neighboring territories to solicit

EPCs, although without radio-tracking data, I cannot rule out the possibility of such forays (e.g., Neudorf et al. 1997, Double and Cockburn 2000). It is also possible that EPCs solicited by females were particularly covert and therefore unlikely to be observed.

Although forced copulations might be uncommon among passerines (reviewed by Gowaty and Buschhaus 1998, Westneat and Stewart 2003), apparent forced copulation attempts have been described in two populations of the American Crow (Kilham 1984; this study). Similar observations of resisted copulation attempts involving incubating females have been documented for two other corvids, the Northwestern Crow (*Corvus caurinus*; Verbeek and Butler 1999) and the Rook (*Corvus frugilegus*; Roskaft 1983); in the Rook, as in the Ithaca population of the American Crow, these attempts sometimes involved multiple males simultaneously.

Even if females unwillingly accept copulations in order to reduce the costs of harassment, they might exercise cryptic post-copulatory choice over the success of the sperm, rejecting that of undesired males (Gowaty and Buschhaus 1998). If female crows exercise such cryptic mate choice, we might expect that they would reject sperm from close relatives (particularly their sons), given the severe disease-mediated survival costs of close inbreeding in this population (Townsend et al. 2009a). Relatedness to the female breeder did not influence the success of prospective extrapair sires, however, and prospective extrapair sires were not more likely to gain paternity with a given female when they were less related to her than she was to her social mate. Three of the extrapair males that gained paternity in this study were adult sons of the female breeder (Townsend et al. 2009a; this study), suggesting that post-copulatory mate choice for the most genetically compatible mates, if it occurs in crows, is imperfect. Another way in which females might bias the outcome of EPC attempts is by accepting EPCs from a relatively small proportion of prospective extrapair males, which are disproportionately successful at siring offspring (Birkhead and Møller 1995, Westneat and Stewart 2003). My observations, though limited, did not support this idea. Only one of the EPC attempts I observed appeared to be passively accepted by the female, but this male gained no paternity in her brood.

Although the patterns of EPP with EPC suggested that certain females might have been involved in EPCs with multiple males in certain group-years, it is unclear whether this possibility resulted from a characteristic of a given breeding female, breeding male, auxiliary male(s), or neighboring male(s). Certain females, such as those paired to a low-quality male, might have been more likely to accept EPCs (Jennions and Petrie 2000, Kempnaers 2007, Mays et al. 2008). Certain males might have been less able to adequately guard their females if they were in poor condition, if a large number of adult male auxiliaries competed with them for paternity, and/or if they were continually harassed by one or more extrapair males from outside of the group. Future work will examine whether the characteristics of breeders and auxiliary birds predict patterns of EPP among broods in this population of American Crows.

Many thanks to the efforts and support of the Crow Research Group: A. B. Clark, K. J. McGowan, D. Robinson, R. Heiss, J. Murray, J. Montagna, T. Wilson, Z. Adaila, J. McGowan, and A. Tringali. M. Savoca assisted with focal observations, and L. Shoenle assisted in the genetic analyses. I. J. Lovette, L. Stenzler, C. Makarewich, and A. Talaba provided support for laboratory work, and A. B. Clark, K. J. McGowan, W. Koenig, and J. Dickinson and the Dickinson lab provided discussions and advice. Support for this work was provided by the National Science Foundation, the National Institutes of Health,

the Animal Behaviour Society, Cornell Sigma Xi Grant-in-Aid of Research, the Frank M. Chapman Memorial Fund, the Kieckhefer Adirondacks Fellowship, the Cooper Ornithological Society, the Wilson Ornithological Society, the Andrew W. Mellon Foundation, an Eloise Gerry Fellowship from Sigma Delta Epsilon/Graduate Women in Science, and the American Association of University Women.

LITERATURE CITED

- AKCAY, E., AND J. ROUGHGARDEN. 2007. Extra-pair paternity in birds: review of the genetic benefits. *Evolutionary Ecology Research* 9:855–868.
- ARNQVIST, G., AND M. KIRKPATRICK. 2005. The evolution of infidelity in socially monogamous passerines: the strength of direct and indirect selection on extrapair copulation behavior in females. *American Naturalist* 165:S26–S37.
- ARNQVIST, G., AND M. KIRKPATRICK. 2007. The evolution of infidelity in socially monogamous passerines: a response to Griffith. *American Naturalist* 169:282–283.
- BIRKHEAD, T. R., AND A. P. MØLLER. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.
- BIRKHEAD, T. R., AND A. P. MØLLER. 1995. Extra-pair copulation and extra-pair paternity in birds. *Animal Behaviour* 49:843–848.
- CLARK, A. B., D. A. ROBINSON, AND K. J. MCGOWAN. 2006. Effects of West Nile virus mortality on social structure of an American Crow (*Corvus brachyrhynchos*) population in New York state. *Ornithological Monographs* 60:65–78.
- DOUBLE, M., AND A. COCKBURN. 2000. Pre-dawn infidelity: females control extra-pair mating in Superb Fairy-Wrens. *Proceedings of the Royal Society of London B* 267:465–470.
- DUNN, P. O., AND J. T. LIFJELD. 1994. Can extra-pair copulations be used to predict extra-pair paternity in birds? *Animal Behaviour* 47:983–985.
- ELIASSEN, S., AND H. KOKKO. 2008. Current analyses do not resolve whether extra-pair paternity is male or female driven. *Behavioral Ecology and Sociobiology* 62:1795–1804.
- GOWATY, P. A., AND N. BUSCHHAUS. 1998. Ultimate causation of aggressive and forced copulation in birds: female resistance, the CODE hypothesis, and social monogamy. *American Zoologist* 38:207–225.
- GRIFFITH, S. C., I. P. OWENS, AND K. A. THUMAN. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology* 11:2195–2212.
- GRIFFITH, S. C. 2007. The evolution of infidelity in socially monogamous passerines: neglected components of direct and indirect selection. *American Naturalist* 169:274–281.
- JENNIONS, M. D., AND M. PETRIE. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* 75:21–64.
- KALINOWSKI, S. T., M. L. TAPER, AND T. C. MARSHALL. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* 16:1099–1106.
- KELLER, L. F., AND D. M. WALLER. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution* 17:230–241.
- KEMPNAERS, B. 2007. Mate choice and genetic quality: A review of the heterozygosity theory, p. 189–278. *In* H. J. Brockmann, T. Roper, M. Naguib, K. Wynne-Edwards, C. Barnard, and J. Mitani [EDS.], *Advances in the study of behavior*. Vol. 37. Academic Press, New York.
- KILHAM, L. 1984. Intra- and extrapair copulatory behavior in American Crows. *Wilson Bulletin* 96:716–717.
- MAYS, H. L., T. ALBRECHT, M. LIU, AND G. E. HILL. 2008. Female choice for genetic complementarity in birds: a review. *Genetica* 134:147–158.
- MCGOWAN, K. J. 2001. Demographic and behavioral comparisons of suburban and rural American Crows, p. 365–381. *In* J. M.

- Marzluff, R. Bowman, and D. Donnelly [EDS.], Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.
- NEUDORF, D. L., B. J. M. STUTCHBURY, AND W. H. PIPER. 1997. Covert extraterritorial behavior of female Hooded Warblers. *Behavioral Ecology* 8:595–600.
- PEDERSEN, M. C., P. O. DUNN, AND L. A. WHITTINGHAM. 2006. Extraterritorial forays are related to a male ornamental trait in the Common Yellowthroat. *Animal Behaviour* 72:479–486.
- R DEVELOPMENT CORE TEAM. 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- ROSKAFT, E. 1983. Male promiscuity and female adultery by the Rook *Corvus frugilegus*. *Ornis Scandinavica* 14:175–179.
- SCHOENLE, L. A., A. K. TOWNSEND, AND I. J. LOVETTE. 2007. Isolation and characterization of microsatellite loci in a cooperatively breeding corvid, the American Crow (*Corvus brachyrhynchos*). *Molecular Ecology Notes* 7:46–48.
- TARR, C. L., AND R. C. FLEISCHER. 1998. Primers for polymorphic GT microsatellites isolated from the Mariana Crow, *Corvus kubaryi*. *Molecular Ecology* 7:253–255.
- TOWNSEND, A. K., A. B. CLARK, K. J. MCGOWAN, E. L. BUCKLES, A. D. MILLER, AND I. J. LOVETTE. 2009a. Disease-mediated inbreeding depression in a large, open population of cooperative crows. *Proceedings of the Royal Society B* 276:2057–2064.
- TOWNSEND, A. K., A. B. CLARK, K. J. MCGOWAN, AND I. J. LOVETTE. 2009b. Reproductive partitioning and the assumptions of reproductive skew models in the cooperatively breeding American Crows. *Animal Behaviour* 77:503–512.
- VERBEEK, N. A. M., AND R. W. BUTLER. 1999. Northwestern Crow (*Corvus caurinus*), no. 407. In A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Philadelphia.
- WESTNEAT, D. F., AND I. R. K. STEWART. 2003. Extra-pair paternity in birds: causes, correlates, and conflict. *Annual Review of Ecology, Evolution, and Systematics* 34:365–396.