Courtship Behaviour in reintroduced California Condors: evidence for extra-pair copulations and female mate guarding

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ABSTRACT

The California Condor *Gymnogyps californianus* is one of world's most critically endangered birds. Beginning in 1992, reintroductions have sought to re-establish wild populations and recent breeding efforts have allowed the opportunity for intensive study of breeding behaviour. Here, we document for the first time the occurrence of extra-pair copulations and female mate guarding in condors. We studied courtship behaviour from late November through to egg-laying (mid-February to early April) when displays and copulations ceased. We quantified displays and copulations by observing focal males during timed observation periods. Courtship behaviour in condors includes male displays, mounting and copulation. Full displays began up to 124 days prior to egg-laying although early pre-breeding displays rarely led to mounting and attempted copulations. Copulations began up to 25 days prior to egg-laying. Females often solicited displays by approaching and interacting with males. Males usually displayed to extra-pair females when their social mate was out of sight. Where pair females were present, they disrupted such displays or copulation attempts. Although extra-pair behaviour was not previously documented in wild condors, this may have been because in observations biased towards nest sites encounters with extra-pair birds are rare. Alternatively, the propensity for such behaviour may be enhanced in the reintroduced population because of increased opportunity for social interaction related to supplementary feeding, mate incompatibility due to limited mate choice or a high degree of genetic relatedness among mates. Whether condors are genetically monogamous remains to be determined.

INTRODUCTION

Birds are unusual among vertebrates in the prevalence of monogamy and extensive male parental care (Lack 1968). However, numerous studies have shown mating within the pair bond to be exceptional among passerine birds (reviewed in Birkhead & Møller 1992; Westneat & Sherman 1997). Strikingly, the prevalence of extra-pair paternity in many socially monogamous passerines has not been mirrored in most monogamous non-passerines (e.g. Decker *et al.* 1993; Korpimäki *et al* 1996; Negro *et al* 1996; Piper *et al.* 1997; Gilbert *et al.* 1998; but see Huyvaert *et al.* 2000). This suggests that factors promoting extra-pair behaviour are lacking or absent in non-passerines. However, at least some non-passerines engage in paternity assurance behaviour such as mate guarding, suggesting that males may perceive potential threats to their paternity even in these species (e.g. Hunter *et al.* 1992; Korpimäki *et al.* 1996; but see Villaroel *et al.* 1998).

We investigated courtship behaviour in a reintroduced population of the California Condor *Gymnogyps californianus*, a large diurnal, vulture currently restricted to southern and central California and northern Arizona. The California Condor is one of the most critically endangered birds in the world (BirdLife International 2000) with a world population of 210 birds including 79 wild and 131 captive individuals (R. Jurek, unpublished data). California Condors are characterised by being at least superficially sexually monomorphic, exhibit extensive parental investment by both sexes and have apparently highly stable long-term pair bonds. Condor pairs remain together throughout the year and maintain exclusive nesting territories centred around nest sites.

Data on courtship behaviour in condors prior to intensive studies in the early 1980s are scant. During his four years of study of birds in southern California, Koford (1953) documented courtship displays on more than 30 occasions but only a single copulation. Wilbur & Borneman (1972) observed eight copulations, only three of which were preceded by displays. During intensive studies of seven pairs in the 1980s, 293 displays were documented, over half (54%) of which led to copulation attempts (Snyder & Snyder 2000). Almost without exception, all displays were performed by males to females. Moreover, there were no observations of extra-pair copulations (although there are no data on the identities of displaying birds). However, condors exhibit a high degree of sociality, particularly at overnight roosts and at feeding sites. Further, observations prior to the 1980s were of unmarked birds while courtship behaviour in the 1980s was largely confined to sites, especially roosts, within the vicinity of condor nest territories. Thus, there may have been some bias towards courtship behaviour between social mates. In this study, we aimed to quantify condor courtship behaviour and its relationship, if any, to egg-laying. Further, we aimed to evaluate the role of females in courtship, particularly in determining the timing and outcome of copulations.

METHODS

We studied condors in southern California during the courtship phase from late November to April in 2001/02 and 2002/03. During the observation period the southern California population of condors (up to 23 birds) held 12 birds of

breeding age (5 males and 7 females). Most observations were made in the southern Los Padres National Forest, Ventura County, at regular roost and supplementary feeding sites but also opportunistically wherever we located condors. The dominant habitat type in the study area was steep-sided coastal chaparral with smaller areas of coastal oak woodland, isolated groves of Big-Cone Douglas-Fir *Pseudotsuga macrocarpa*, and open grassy potreros. Roost sites were mainly on cliffs and tall dead Big-cone spruce trees.

To quantify condor courtship and mating behaviour, we made timed observations of the behaviour of adult males (N=5) to determine display and copulation rates (events/hr^{-1}). Individual focal samples lasted a minimum of 15 minutes during which all courtship behaviours were recorded and timed. Additionally, for observations of less than 15 minutes we recorded condor courtship opportunistically. Males (N=5) of breeding age (range 7-9 years) in the southern California population were the unit of analysis in determining behavioural rates. In all cases, we noted the time, location, duration of courtship, outcome and identity of participants. Condor courtship consists of several behaviours, principally synchronous pair-flights, wing-out courtship displays, mounting and copulation, as well as mutual grooming (Snyder & Schmitt 2002). In this study we focus on courtship displays, mounting and copulation as these are relatively easy to record and quantify. Wing-out displays, mounting and copulation have been well described by previous authors both in the wild (eg. Koford 1953; Snyder & Snyder 2000; Snyder & Schmitt 2002) and captivity (Cox *et al* 1993; Harvey *et al* 1996). During the 2001/02 and 2002/03 courtship periods we observed condors for a total of 100.2 and 149.6 hours respectively (98.3 and 146.9 focal hours).

RESULTS

We documented displays involving all 12 adult birds (5 males and 7 females) in the southern California population. Condor displays averaged 53 seconds in duration (range 4-182) over the two years combined. Mounts and copulations averaged 76 (range 2-270) and 5 (range 3-8) seconds in duration over the same period. Displays were recorded over a 16 week period, beginning in late November and continuing up until egg-laying in mid-March in 2001/02 (Table 1). In 2002/03, the first displays were recorded about one month later and extended over a 10-week period to early April. Only 21.3% of displays led to mounting and fewer still (9.4%) to attempted or successful copulations. Of 30 documented copulations, 23% were not preceded by displays, 47% were preceded by displays, while in 30% of cases it was unknown whether copulations were preceded by displays or not.

Copulations took place over a four-week period from 19 January to 21 March in 2002/03 and 16 February to 4 April in 2002/03 (Table 1). Male display rates peaked at 10 and five weeks prior to egg-laying, declining in the weeks leading up to egg-laying. Display and copulation rates were higher in 2001/02 when three pairs laid eggs than in 2002/03 when only a single pair nested (Table 2). Although most courtship events were between social mates, males often displayed to, mounted and occasionally copulated with extra-pair females (Table 3).

Table 1. Timing of California Condor courtship events (N=5 males) in relation to egg-laying date. Data shown are days to egg-laying of earliest and latest display and copulation recorded (weeks to egg-laying in parentheses).

	Displays		Copulations	
Year	First	Last	First	Last
2002	124 (16)	2	25 (4)	1
2003	74 (10)	2	16 (3)	1

Table 2. Courtship rates in California Condors (N=5 males). All events included mounts and copulations without prior displays)

	Behavioural rates (events/hr^{-1})		
Year	Display	Copulation	All events
2002	0.68	0.17	0.78
2003	0.40	0.03	0.46
Other species*			
Eurasian kestrel		0.72	
American kestrel		0.00-3.85	
Red Kite		0.24-0.47	

*Other species: data from Korpimäki et al 1996; Villaroel et al 1998; Mougeot 2000.

Table 3. Proportion of California Condor within-pair and extra-pair courtship events (number of events in parentheses). Other = events where the identity of both birds was not determined.

	Displays	Copulations	All events*
Event type	(174)	(30)	(206)
Within-pair	0.59	0.77	0.58
Extra-pair	0.34	0.23	0.31
Other	0.07	0.00	0.10

*Includes mounts/copulations without prior displays

Based on our preliminary findings, California Condors appear to have a relatively short copulatory window (4 weeks) with a low to moderate rate of copulation in relation to those recorded for old-world vultures (Table 4). However, extra-pair behavioural rates (displays and copulations) appear to be much higher than previously recorded in condors as well other vulture species (Table 4). Pair males engaging in extra-pair courtship generally did so when their social mate was out of sight. Females took an active role, determining the initiation and outcome of courtship events. Some females actively solicit extra-pair displays and copulations by approaching, grooming or crouching in front of males other than their social mate. Pair females appear to be particularly vigilant in disrupting extra-pair courtship events and most disrupted events (81%) were extra-pair.

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Table 4. Copulatory behaviour in California Condors (N=4) in relation to some Old-World vultures*

Species	Copulation period	Copulation rate**	% EPCs
California condor	-25 to -1	low-mod	23.0
Bearded vulture	-90 to +87	high	0.5
Egyptian vulture	-25 to FED	high	2.6
Cape griffon	-90 to +140	100	0.5

* Data from Negro & Grande (2001)
* Based on number of copulations/female/clutch. Copulation rates were described as high if copulation was described as frequent (see Negro & Grande 2001)

DISCUSSION

In contrast to data from the well-studied wild condor population of the 1980s (Snyder & Snyder 2000; Snyder & Schmitt 2002), we found that fewer displays led to successful mounting (21.3% vs. 54%) in the reintroduced southern California study population. Further, we found several instances where copulation was not preceded by displays. Thus, our data appear to agree more closely with the observations of Koford (1953) and Wilbur & Borneman (1972).

Relative to many raptors and other Old-World vulture species (reviewed in Negro & Grande 2001), copulation rates in condors appear to be somewhat lower while the period over which copulations take place is more restricted (but similar to Egyptian vulture *Neophron percnopterus* at −25 days to egg-laying with some events taking place after clutch completion; Donázar *et al* 1994). However, we document extra-pair displays and copulations for the first time in this species. Indeed, our data, although admittedly limited to date, suggest that extra-pair courtship activities make up a sizeable proportion of all events. Further, females both actively solicit extra-pair displays and copulations while pair females attempt to mate guard by disrupting most extra-pair courtship attempts.

One outstanding question resulting from this study is why extra-pair courtship is more prevalent today (23%) as opposed to the historical population where such behaviour was undocumented? We suggest three hypotheses, neither mutually exclusive, which might explain this apparent discrepancy between the reintroduced population and the historic population. (1) Extra-pair courtship did occur in the historic population but was not documented because observations were heavily weighted towards behaviour at or near nesting territories (1980s) or the identity of individual birds was unknown (pre-1980s). In the reintroduced southern California population most courtship events were recorded at supplementary feeding sites, roosts and cliff sites away from nesting territories. Only 10% of all courtship events took place in the vicinity of nest sites and all but one involved social mates. This suggests that extra-pair events could have occurred in the 1980s away from nesting territories and were undocumented. (2) Alternatively, extra-pair courtship behaviour is artificially high in the present reintroduced southern California population due to

increased sociality and opportunities for interaction between extra-pair adults related to intensive supplementary feeding at a restricted number of sites. Further, most adult condors are in the process of forming long-term pair bonds while small population size has resulted in very limited options for choosing mates. The latter may occasionally result in mate incompatibility, where the alternative is to forego breeding because of the lack of suitable mates. While the 1980s population also undoubtedly suffered effects of small population size, potential negative effects of limited mate choice may have been negligible because the few remaining pairs were long established, experienced breeders. If mate incompatibility is an important factor in promoting extra-pair behaviour in the present population, the level of extra-pair activity should decline in future as birds have more potential mates available and are forced into fewer poor choices of social mates. (3) Increased levels of extra-pair behaviour may result from birds attempting to avoid the negative effects of pairing with genetically similar mates (Blomqvist *et al* 2002).

As the genetic relationships of all reintroduced condors are known, we have the opportunity to test this hypothesis in the field. If condors are promiscuous this may have important implications for population management as increased variance in reproductive success between males would result in a smaller effective population size than would be expected if birds were strictly monogamous. Microsattelite DNA analysis of wild-born chicks and putative parents will allow us to determine whether condors are genetically monogamous, identify parentage and, if reproductive success is significantly skewed towards some individuals, make recommendations for population management to increase effective population size.

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REFERENCES

BIRDLIFE INTERNATIONAL 2000. *Threatened Birds of the World.* Lynx Edicions and BirdLife International. Barcelona and Cambridge, UK.
BIRKHEAD, T.R. & A.P. MØLLER 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences.* Academic Press.
BLOMQVIST, D., M. ANDERSON, C. KÜPPER, I.C. CUTHILL, J. KIS, R.B LANCTOT, B.K. SANDERCOCK, T. SZÉKELY, J. WALLANDER & B. KEMPENAERS 2002. Genetic similarity between mates and extra-pair parentage in three species of shorebird. *Nature* 419, 613-615.
COX, C.R., V.I. GOLDSMITH & H.R. ENGELHARDT 1993. Pair formation in California Condors. *Amer. Zool.* 33, 126-138.
DECKER, M.D., P.G. PARKER, D.J. MINCHELLA & K.N. RABENOLD 1993. Monogamy in black vultures: genetic evidence from DNA fingerprinting. *Behav. Ecol.* 4, 29 – 35.
DONÁZAR, J.A., O. CEBALLOS & J.L. TELLA 1994. Copulation behaviour in the Egyptian vulture. *Bird Study* 41, 37-41.

GILBERT, L., T. BURKE & A. KRUPA 1998. No evidence for extra-pair paternity in the western gull. *Mol. Ecol.* 7, 1549 - 1552.

HARVEY, N.C., K.L. PRESTON & A.J. LEETE 1996. Reproductive behavior in captive California Condors (*Gymnogyps californianus*). *Zoo Biology* 15, 115-125.

HUNTER, F.M., T. BURKE & S.E. WATTS 1992. Frequent copulation as a method of paternity assurance in the northern fulmar. *Anim. Behav.* 44, 149 – 156.

HUYVAERT, K.P., D.J. ANDERSON, T.C. JONES, W.R. DUAN & P.G. PARKER 2000. Extra-pair paternity in waved albatrosses. *Mol. Ecol.* 9, 1415 – 1419.

KOFORD, C.B. 1953. The California Condor. Natl. Audubon Soc. Res. Report No. 4, 1-154.

KORPIMÄKI, E., K. LAHTI, C.A. MAY, D.T. PARKIN, G.B. POWELL, P. TOLONEN & J.H. WETTON 1996. Copulatory behaviour and paternity determined by DNA fingerprinting in kestrels: effects of cyclic food abundance. *Anim. Behav.* 51, 945-955.

LACK, D. 1968. *Ecological Adaptations for Breeding in Birds.* Methuen, London.

MOUGEOT, F. 2000. Territorial intrusions and copulation patterns in red kites, *Milvus milvus*, in relation to breeding density. *Anim. Behav.* 59, 633-642.

NEGRO, J.J. & J.M. GRANDE 2001. Territorial signaling: a new hypothesis to explain frequent copulation in raptorial birds. *Anim. Behav.* 62, 803-809.

NEGRO, J.J., M.R. VILLAROEL, J.L. TELLA, U. KUKNLEIN, J.A. DONÁZAR & D.M. BIRD 1996. DNA fingerprinting reveals a low incidence of extra-pair fertilizations and intraspecific brood parasitism in the lesser kestrel. *Anim. Behav.* 51, 921-930.

PIPER, W.H., D.C. EVERS, M.W. MEYER, K.B. TISCHLER, J.D. KAPLAN & R.C. FLEISCHER 1997. Genetic monogamy in the common loon (*Gavia immer*). *Behav. Ecol. Sociobiol.* 41, 25 – 31.

SNYDER, N.F.R. & N.J. SCHMITT 2002. California condor (*Gymnogyps californianus*), In *The Birds of North America*, No. 610 (Poole, A. & Gill, F. Eds.). The Birds of North America, Inc., Philadelphia, PA.

SNYDER, N.F.R. & H.A. SNYDER 2000. *The California condor, a saga of natural history and conservation.* Academic Press, London, UK.

VILLAROEL, M., D.M. BIRD & U. KUNHLEIN 1998. Copulatory behaviour and paternity in the American kestrel: the adaptive significance of frequent copulations. *Anim. Behav.* 56, 289-299.

WESTNEAT, D.F. & P.W. SHERMAN 1997. .Density and extra-pair fertilizations in birds: a comparative analysis. Behav. Ecol. Sociobiol. 41, 205 – 215.

WILBUR, S.R. & J.C. BORNEMAN 1972. Copulation by California Condors. *Auk* 89, 444-445.

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