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FIRST RECORD OF DOUBLE BROODING BY THE COMMON RAVEN

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The Common Raven (*Corvus corax*) ranges throughout the Holarctic, but many life-history attributes of this species, including mean lifespan, age at first breeding, age-specific fecundity, and other important variables, remain poorly documented (Boarman and Heinrich 1999). During the spring of 2001, we observed a single pair of ravens successfully rear two broods from a nest located on the campus of the University of California, Riverside. Prior to our observations, ravens had been known to produce only replacement clutches after loss of eggs (Bowles and Decker 1930) or nestlings (Stiehl 1985). In the case we describe below, a pair of ravens raised a second brood apparently in response to a short period of fledgling dependence rather than producing a second clutch in response to a loss of eggs or nestlings. This constitutes the first record of double brooding for the Common Raven.

We located the raven nest on a third-floor window awning approximately 75 m north of Ellstrand's office in an adjacent building on campus. We monitored the nesting behavior from Ellstrand's office and from the grounds nearby, observing the ravens successfully rear two broods. Both broods fell within the usual dates for the raven nesting season (Stiehl 1985, Ratcliffe 1997, Boarman and Heinrich 1999). The pair initiated nesting relatively early in the spring of 2001, with incubation beginning approximately 4 March (Figure 1). This first brood fledged around 3 May. At this time we observed a family group of ravens consisting of two fledglings and two adults in the natal territory.

The fledglings were absent from the natal territory by 15 May when we first observed incubation of the second brood. On the basis of the typical incubation period of 3 weeks (Boarman and Heinrich 1999), we estimate that laying of the second clutch began as early as 9 May. Three nestlings from the second brood were visible by 5 June, and they reached nearly adult size in early July. The second brood fledged on 4 July and accompanied the adults in the natal territory during the following week.

Raven fledglings normally remain in their natal territory for a period of 1 to 6 weeks while the parents continue feeding them (Ratcliffe 1997, Boarman and Heinrich 1999, Webb 2001). In the case of the Riverside nest, both broods remained in the natal territory for less than a week after fledging, a relatively short period. Short periods of fledgling dependence are most often associated with mortality before independence is reached (Verhulst and Hut 1996). Raven fledglings fly poorly and often succumb to predators (Ratcliffe 1997, Webb 2001). Most mortality (87%) of hatching-year ravens occurs when fledglings are dependent (Webb 2001). In the Mojave Desert, Coyotes (Canis latrans) account for at least 33% of raven fledgling mortality (Webb 2001). The University of California Riverside campus hosts a population of Coyotes and other mesopredators including the Gray Fox (Urocyon inereoargenteus), Bobcat (Felis rufus), and feral domestic cat (Felis silvestris catus). When the fledglings from the first and second brood appeared missing, we searched the natal territory but found no carcasses.

Renesting can occur when the environment remains favorable and nesting birds retain enough energy for reproduction. Previous studies found that relative reproduc-

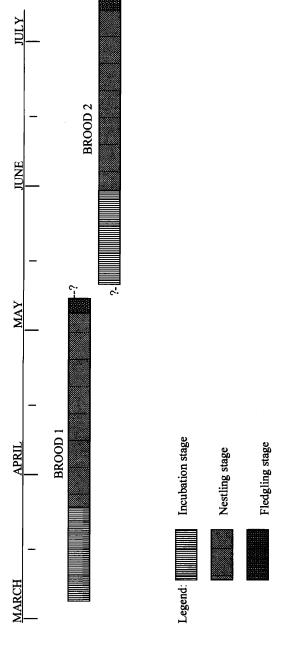


Figure 1. Chronology of a Common Raven nest at Riverside, California, in 2001.

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tive efforts of consecutive broods are correlated (Smith et al. 1987, Linden 1988, Conrad and Robertson 1992), and the probability of renesting depends in some degree on the amount of post-fledging care (Hegner and Wingfield 1987, Tinbergen 1987). In the case of the Riverside nest, the short fledgling-dependence period (a likely result of fledgling mortality) probably combined with an abundance of nearby anthropogenic resources to facilitate renesting.

Although neither adult was marked, we are reasonably confident that the second brood was produced by the same pair of birds. Ravens are strongly territorial (Armstrong 1958, Craighead 1979, Davis and Davis 1986, Cramp and Perrins 1994) and defend their nesting territories throughout the year (Ratcliffe 1997), making the invasion of a second pair unlikely. Invasion of the nesting territory by a new pair would require displacement of the existing pair. Because suitable nest locations are abundant in the area, a new pair would be more likely to establish a separate territory rather than to displace the existing pair.

Death of one nesting adult followed by rapid replacement with a new mate is an unlikely explanation because survival rates of adult ravens are believed to be high (Ratcliffe 1997). Although rapid remating has been noted previously (Stiehl 1985, Ratcliffe 1997), it has been observed only after early nest failure, not after successful fledging, and never as late as May (Boarman and Heinrich 1999). Extreme wildlife hazards capable of killing an entire raven family (e.g., poisoned carcasses, hunters) occur in some regions of California (Webb 2001) but are absent from the suburban environment of Riverside. Thus, we believe that mortality of the entire initial family group followed by rapid replacement with another nesting pair is also unlikely.

Genetically influenced behavioral differences might explain the occurrence of the second brood. Double brooding could be more common in the small subspecies of raven prevalent in California (C. c. clarionensis) (Rea 1983, 1986) but not previously detected because most previous studies of ravens in North America concern the widespread C. c. principalis. Omland et al. (2000) suggested that the majority of ravens from California are genetically divergent from a holarctic clade consisting primarily of C. c. principalis and other subspecies.

Several other North American species of the tribe Corvini have been known to raise more than one brood (Ehrlich et al. 1988), including the Pinyon Jay (Gymnorhinus cyanocephalus), Blue Jay (Cyanocitta cristata), Brown Jay (Cyanocorax morio), American Crow (Corvus branchyrhynchos), and Northwestern Crow (Corvus caurinus).

We thank William I. Boarman for reviewing an earlier version of the manuscript, which was also greatly improved by thoughtful comments provided by Michael A. Patten and Brian L. Sullivan.

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Accepted 28 October 2002