

MATE REPLACEMENT AND ALLOPARENTAL CARE IN FERRUGINOUS HAWK (*BUTEO REGALIS*)

—Alloparental care (i.e., care for unrelated offspring) has been documented in various avian species (Maxson 1978, Smith et al. 1996, Tella et al. 1997, Lislevand et al. 2001, LITERAK and Mraz 2011). A male replacement mate that encounters existing broods has options, which include alloparental care or infanticide. Infanticide may be beneficial in some species (Rohwer 1986, Kermott et al. 1990), but in long-lived avian species, like the ferruginous hawk (*Buteo regalis*) that do not renest within a season, infanticide might be detrimental. Adoption and rearing success likely provide direct evidence of competence of replacement mates as potential parents for future seasons, a benefit that might outweigh the investment of time and effort associated with adoption and rearing (after Rohwer 1986). Anticipated mating opportunity at the cost of adoption (Gori et al. 1996, Rohwer et al. 1999) may explain step-parental benevolence and therefore, in such a scenario would enhance individual fitness through subsequent recruitment of related young.

Male replacement mates have been documented for peregrine falcon (*Falco peregrinus*), northern goshawk (*Accipiter gentilis*), and at least 13 non-raptorial (11 Passeriformes, 1 Galliformes, and 1 Piciformes) avian species (Rohwer 1986, Meek and Robertson 1991, Lislevand et al. 2001); in all cases, potential for renesting existed and replacement males were exposed mostly to eggs rather than young. However, ferruginous hawks are noted as “apparently” monogamous with no evidence of alloparental behavior (Bechard and Schmutz 1995). Here we report an instance of adoption of four ferruginous hawk nestlings by an adult male ferruginous hawk following death of the male parent. We document execution of parental duties by the replacement male conjointly with the female parent.

As part of a reproductive ecology study (South Dakota State University Institutional Animal Care and Use Committee protocol #12–057E), we were monitoring active raptor nests ≥ 1 times per week after nest initiation in south-central North Dakota. On 29 June 2013 in Logan County, North Dakota (14T 5131661 N, 472922 W), we observed a dead adult male ferruginous hawk on a paved road within 30 m of an active tree nest that had been monitored since 15 April 2013. The carcass was fresh and we determined that vehicular collision was the probable cause of death. The nest in the immediate vicinity contained four nestlings (estimated ages were 21 to 24 days) on the day of the aforesaid observation. Previously, both parents actively defended the nest when approached, but after finding the dead male, only the nesting adult female ferruginous hawk defended the nest. We intensified nest monitoring after this observation and visited the nest daily to observe activity and to determine the fate of the nestlings. Over the next 13 days, only the adult female ferruginous hawk fed nestlings and defended the nest. On 12 July 2013 while banding the nestlings, we observed a male ferru-

ginous hawk defending the nest. In alliance with the female it hovered and produced territorial vocalizations and attempted perfunctory swoops at the researchers. During subsequent nest visits ($n = 18$) until fledging, we observed participation by the male ferruginous hawk in nest defense (hovering while vocalizing) and in food procurement. We observed the male deliver food to the nest ($n = 4$) or dropping it nearby ($n = 2$) after which the female would take the dropped food to the nest. The female seemed apprehensive with researcher presence and observations were terminated at this point. On 22 July 2013 we considered the nestlings to have fledged, and on 1 August 2013, we documented all four fledglings alive at and near the nest as we concluded our observations.

Considering the above sequence of events, we concluded that the most likely scenario was that the dead ferruginous hawk was the male parent and the resident female parent received assistance from a replacement male whose familial relationship with the female parent could not be established due to the empirical nature of our evidence.

Instances of mate replacement are frequent and widespread throughout raptor families (Newton 1979); however, brood adoption observations frequently lack quantitative information on provisioning of partial versus complete parental care (Meek and Robertson 1991). Although a fairly common phenomenon (Rohwer 1986) in non-raptorial species (Odum 1941, Kilham 1977, Nolan 1978, Martin 1984), instances of adoption of unrelated young in raptorial species are rare (MacIntyre 1960, Newton 1979). Adoption is commonly considered maladaptive and a consequence of misdirected parental care (Gori et al. 1996). However, partial or complete alloparental care could be adaptive when potential exists for future mating opportunities. Cost of infanticide for the replacement male may be maladaptive as it might restrict gaining territory and cross-season potential of mating (Rohwer et al. 1999), both of which may be accomplished through adoption. Renesting in a single breeding season has not been reported in ferruginous hawks (Bechard and Schmutz 1995) due to insufficient time to complete a second breeding attempt. Investing in care for unrelated young under such circumstances may seem altruistic (Brown 1975). Display of parental care by the replacement male ferruginous hawk that we witnessed may be an adaptive mechanism to facilitate pairing in the current year or potential mating in the following breeding season.

Our observations could be adoption by a male of an unrelated brood or might be cooperative in nature. Ferruginous hawks have been suspected as cooperative breeders (Bechard and Schmutz 1995, Kimball et al. 2003) and it is possible that the adoption behavior we observed was performed by a related male. In diurnal raptors that are suspected cooperative breeders (42 of 304 species; 14%), presence of an extra male during the breeding season has been confirmed in 60% ($n = 25$) of species (Kimball et al. 2003). Though information on relatedness of extra males to breeding females is limited, copulation has been documented in 52% ($n = 13$) of those

species, 77% ($n = 10$) of which also showed behavior that improved the probability of rearing offspring successfully (after Kimball et al. 2003). If the replacement male was related to the female, adoption still could be viewed as adaptive even without the intended benefit of cross-season mating. The scenario we present and the speculations thereof are based on observational evidence and due to the contingent nature of such observations in free-ranging ferruginous hawks, a declining grassland species (Houston and Schmutz 1999). It is important to better understand and conduct dedicated research including genetic level analyses on the topic for more conclusive assertions. The described adaptive mechanism of brood adoption may contribute to recruitment in declining populations of grassland obligate raptors like the ferruginous hawk.

Our study was funded by North Dakota Game and Fish Department, State Wildlife Grant (T-36-R; CFDA # 15.634). Additional support was provided by the Department of Natural Resource Management and the Agricultural Experiment Station at South Dakota State University. W. Keeley reviewed an earlier draft of this manuscript. E. Morata and T. Michels provided technical support. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any mention of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U. S. Government.—*Shubham Datta*^{1,4}, *Will M. Inselman*¹, *Jonathan A. Jenks*¹, *Kent C. Jensen*¹, *Christopher C. Swanson*² *Robert W. Klaver*³, *Indrani Sasmal*¹, and *Troy W. Grovenburg*¹. ¹ Department of Natural Resource Management, South Dakota State University, Box 2140B SNP 138, Brookings, SD 57007, USA; ² U.S. Fish and Wildlife Service, 1 First Street SW, Kulm, ND 58546, USA; ³ U.S. Geological Survey, Iowa Cooperative Fish and Wildlife Research Unit, Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA 50011, USA; ⁴ Corresponding author e-mail address: shubham.datta@sdstate.edu.

LITERATURE CITED

- Bechard, M. J., and J. K. Schmutz. 1995. Ferruginous hawk (*Buteo regalis*). Number 172 in A. Poole and F. Gill, editors. The birds of North America. Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.
- Brown, J. L. 1975. The evolution of behavior. W. W. Norton and Company Inc., New York, New York, USA.
- Gori, D. F., S. Rohwer, and J. Caselle. 1996. Accepting unrelated broods helps replacement male yellow-headed blackbirds attract mates. *Behavioral Ecology* 7:49–54.
- Houston, C. S., and J. K. Schmutz. 1999. Changes in bird populations on Canadian grasslands. *Studies in Avian Biology* 19:87–94.
- Kermott, L. H., L. S. Johnson, and H. Brinton. 1990. Brood adoption and apparent infanticide in a north-temperate house wren population. *Wilson Bulletin* 102:333–336.
- Kilham, L. 1977. Altruism in nesting yellow-bellied sapsucker. *Auk* 94:613–614.
- Kimball, R. T., P. G. Parker, and J. C. Bednarz. 2003. Occurrence and evolution of cooperative breeding among the diurnal raptors (Accipitridae and Falconidae). *Auk* 120:717–729.
- Lislevand, T., G. B. Gronstol, I. Byrkjedal, and J. E. Hafsmo. 2001. Mate replacement and male brood adoption in lapwings *Vanellus vanellus*. *Bulletin-Wader Study Group* 95:55–58.
- Literak, I., and J. Mraz. 2011. Adoptions of young common buzzards in white-tailed sea eagle nests. *Wilson Journal of Ornithology* 123:174–176.
- Macintyre, D. 1960. Nature notes of a highland gamekeeper. Seeley, Service and Co., London, UK.
- Martin, K. 1984. Reproductive defense priorities of male willow ptarmigan (*Lagopus lagopus*): enhancing mate survival or extending paternity options? *Behavioral Ecology and Sociobiology* 16:57–63.
- Maxson, S. J. 1978. Evidence of brood adoption by ruffed grouse. *Wilson Bulletin* 90:132–133.
- Meek, S. B., and R. J. Robertson. 1991. Adoption of young by replacement male birds: an experimental study of eastern bluebirds and a review. *Animal Behaviour* 42:813–820.
- Newton, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, South Dakota, USA.
- Nolan, V. Jr. 1978. The ecology and behavior of prairie warbler *Dendroica discolor*. Ornithology Monograph 26. American Ornithologists' Union, Washington, D.C., USA.
- Odum, E. P. 1941. Annual cycle of the black-capped chickadee. *Auk* 58:314–333.
- Rohwer, S. 1986. Selection for adoption versus infanticide by replacement “mates” in birds. Pages 353–395 in R. F. Johnston, editor. *Current ornithology*. Springer, New York, New York, USA.
- Rohwer, S., J. C. Herron, and M. Daly. 1999. Stepparental behavior as mating effort in birds and other animals. *Evolution and Human Behavior* 20:367–390.
- Smith, H. G., L. Wennerberg, and T. V. Sachantz. 1996. Adoption or infanticide: options of replacement males in the European starling. *Behavioral Ecology and Sociobiology* 38:191–197.
- Tella, J. L., M. G. Forero, J. A. Donazar, J. J. Negro, and F. Hiraldo. 1997. Non-adaptive adoptions of nestlings in the colonial lesser kestrel: proximate causes and fitness consequences. *Behavioral Ecology and Sociobiology* 40:253–260.

Submitted 15 September 2014. Accepted 29 April 2015.
Associate Editor was M. Rumble.