

TABLE 1. Summary of NPA behavior at 4 nests of the Grasshopper Sparrow.

Nest	Nestling ages observed <sup>1</sup>	Min observed	NPA age	Nestling age with NPA <sup>2</sup>	No. NPA trips/total
3G1	3-7	1,140	Juvenile	7	7/46
4G9	2-3	439	Juvenile	2	2/22 <sup>3</sup>
				3	8/34
4G12	3-5	662	Adult	4	3/30
4G14	2-5	1,234	Adult	3	10/20
				4	8/19
				5	10/28

<sup>1</sup> Nestling ages (in days) in which observations were made.

<sup>2</sup> Nestling ages in which NPAs participated.

<sup>3</sup> Two juvenile NPAs, 1 trip each.

Swallows may potentially usurp nest sites (Crook and Shields 1987, Lombardo 1985). Such an explanation does not appear to hold for the Grasshopper Sparrows. Nest sites are abundant on the open prairie (Kaspari unpubl. data) and NPAs, which consist of both adults and juveniles, apparently are not harmful to nestlings. Grasshopper Sparrows also appear to screen nest visitors on the basis of provisioning abilities.

NPAs may decrease parental males' provisioning responsibilities. An alternate explanation is that this "neglect" facilitates the undisturbed approach of the NPAs (see also Price et al. 1983). Lack of philopatry in migratory populations may prevent the evolution of kin-based altruism among adults. Similarly, high juvenile mortality in the Grasshopper Sparrow (eggs have only a 0.38 probability of producing a fledgling; Kaspari unpubl. data) reduces the likelihood of juvenile help by reducing the pool of kin available to help with the second brood.

NPAs appear to be fairly common among bird populations, but occur at low frequency within populations. Such behavior may be a precursor to both al-

truistic associations (i.e. "helping"; Woolfenden and Fitzpatrick 1984) and exploitative interactions (e.g. intraspecific brood parasitism; Brown 1984). We encourage the documentation of NPAs at nests of other migratory birds. Collectively, such long-term studies should increase our understanding of intraspecific interactions in the breeding season.

We appreciate discussions with many of the faculty and graduate students at the University of Arizona. We gratefully acknowledge the support of A. Joern, J. Janovy Jr., the Cedar Point Biology Station, The Nature Conservancy, and grants from the School of Biological Sciences of the University of Nebraska.

#### LITERATURE CITED

- BROWN, C. R. 1984. Laying eggs in a neighbor's nest: benefits and costs of colonial nesting in swallows. *Science* 224: 518-519.
- CROOK, J. R., & SHIELDS, W. M. 1987. Non-parental nest attendance in the Barn Swallow (*Hirundo rustica*): helping or harassment? *Anim. Behav.* 35: 991-1001.
- LOMBARDO, M. P. 1985. Mutual restraint in Tree Swallows: a test of the TIT FOR TAT model of reciprocity. *Science* 227: 1363-1365.
- MAYFIELD, H. F. 1975. Suggestions for calculating nesting success. *Wilson Bull.* 87: 456-466.
- PRICE, T., S. MILLINGTON, & P. GRANT. 1983. Helping at the nest in Darwin's finches as misdirected parental care. *Auk* 100: 192-194.
- PLYLE, P., S. N. G. HOWELL, R. P. YUNICK, & D. F. DESANTE. 1987. Identification guide to the North American passerines. Bolinas, California, Slate Creek Press.
- SKUTCH, A. F. 1961. Helpers among birds. *Condor* 63: 198-226.
- WOOLFENDEN, G. E., & J. W. FITZPATRICK. 1984. The Florida Scrub Jay: demography of a cooperatively breeding bird. Princeton, New Jersey, Princeton Univ. Press.

#### Sex Ratios of Fledgling Golden Eagles

THOMAS C. EDWARDS JR.,<sup>1,2</sup> MICHAEL W. COLLOPY,<sup>1</sup> KAREN STEENHOF,<sup>3</sup>  
AND MICHAEL N. KOCHERT<sup>3</sup>

<sup>1</sup>Department of Wildlife and Range Sciences, University of Florida, Gainesville, Florida 32611 USA, and

<sup>3</sup>Snake River Birds of Prey Research Project, Bureau of Land Management,  
3948 Development Avenue, Boise, Idaho 83705 USA

The onset of effective incubation prior to completion of the clutch in many avian species establishes

an age and size hierarchy. The older, larger nestlings can outcompete their younger siblings for parent-provided resources. During periods of food stress, the competitive advantage enjoyed by older nestlings allows them to control access to limited resources, which prevents younger nestlings from receiving adequate resources for survival. Brood reduction of this nature

<sup>2</sup> Present address: U.S. Fish and Wildlife Service, Utah Cooperative Fish and Wildlife Research Unit, Utah State University, Logan, Utah 84322-5210 USA.

TABLE 1. Number of fledgling male and female Golden Eagles (1970–1984), Snake River Birds of Prey Area, Idaho.

Year	Male	Female	No. broods	Sex ratio (Male : female)	% Males	G-value <sup>a</sup>
1970	18	23	23	0.782	43.9	0.589
1971	23	25	28	0.920	47.9	0.081
1972	9	7	10	1.285	56.2	0.229
1973	13	5	13	2.600	72.2	3.387
1974	12	4	11	3.000	75.0	3.806
1975	9	13	15	0.692	40.9	0.684
1976	7	10	11	0.700	41.2	0.488
1977	17	9	18	1.888	65.4	2.362
1978	23	15	23	1.533	60.5	1.632
1979	16	6	14	2.667	72.8	4.401*
1980	14	11	14	1.272	56.0	0.340
1981	7	0	5	— <sup>b</sup>	100.0	6.917**
1982	3	1	3	3.000	75.0	— <sup>c</sup>
1983	10	2	7	5.000	83.3	5.097*
1984	5	3	6	1.667	62.5	0.424

<sup>a</sup> Williams' (1976) correction for small samples applied, \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

<sup>b</sup> Division by 0.

<sup>c</sup> Small sample size precluded statistical analysis.

occurs in a variety of contexts, ranging from a passive process of parental indifference and nonaggressive competition among young (Newton 1979, Werschkul 1979, Safriel 1981) to more aggressive processes where older nestlings actively participate in the death of younger siblings (e.g. siblicide; see review by Mock 1984). Although it generally is agreed that competition for parent-provided food is the underlying factor responsible for competitively induced brood reduction, the relative importance of proximate factors such as size disparities between siblings (Spellerberg 1971, Edwards and Collopy 1983), food size (Mock 1985), and food amount (Gargett 1977) varies.

Edwards and Collopy (1983) previously examined the effect of hatching asynchrony, offspring sex, and hatching sequence on the probability of siblicide in Golden Eagles (*Aquila chrysaetos*) with a brood size of two. They suggested that, if parent-provided food was limited and the ability to control access to this food was size related, siblicide was more likely to occur in two-chick broods where a female hatched before a male (F-M). Size differences in M-M, F-F, and M-F hatching sequences were smaller, making it less likely that the older nestling could exclude the younger from parent-provided resources and less likely that siblicide would occur. This increased tendency for the occurrence of siblicide in F-M broods should be manifest in population-level fledgling sex ratios. Specifically, the proportion of fledgling males should be lower in years of poor prey availability than in good years. An underlying assumption of this prediction is that the sex ratio at hatching is not biased in favor of males. Although specific hatching sex ratios of Golden Eagles are not known, data from other fal-

coniforms suggests that hatching sex ratios do not deviate from 1:1 in falconiforms (Newton 1979: table 2).

Research on Golden Eagles was conducted (1970–1984) in the Snake River Birds of Prey Area (BOPA) located south of Boise, Idaho (see U.S. Department of Interior 1979 for a detailed description of the area). We visited nests at the end of the brood-rearing period, and counted the nestlings present. Nestlings that were at least 52 days old, 80% of the mean fledgling age for Golden Eagles (Steenhof and Kochert 1982, Steenhof 1987), were considered fledglings. Estimates of mass (g) and footpad length (mm) for each fledgling were used to sex the young (Edwards and Kochert 1986). The abundance of black-tailed jack rabbits (*Lepus californicus*), the principal food of eagles nesting in the BOPA, was estimated from a combination of spotlighting transects (Smith and Nydegger 1985) and counts by raptor survey crews (U.S. Department of Interior 1979).

Log-likelihood ratio tests (G-test; Sokal and Rohlf 1981: 695) were used to test whether fledgling sex ratios (No. males/No. females) for each year and for all years combined deviated from 1:1. G-values were adjusted using Williams' (1976) correction for small sample sizes prior to ascertaining significance. Runs tests (Sokal and Rohlf 1981: 783) were used to determine whether fledgling sex ratio and jack rabbit density was random with respect to time. We used a 0.05 level of significance for all statistical tests.

Fledgling sex ratios ranged from a low of 0.69:1 in 1975 to a high of 5:1 in 1981 (Table 1). Females outnumbered males in only 4 of 14 years. An overall bias in favor of males was evident when data were com-

bined across years ( $G = 8.474$ ,  $df = 1$ ,  $P = 0.004$ ). When individual years were considered, however, only 3 of 14 years exhibited significant deviations from 1:1 (Table 1). All significant deviations favored males.

The temporal pattern in sex ratio suggests an overall male bias (Fig. 1), but the pattern was not significant statistically (runs test,  $n_1 = 4$ ,  $n_2 = 11$ ,  $u = 4$ ,  $0.05 < P < 0.1$ ). In contrast, change in jack rabbit density was nonrandom with respect to time (runs test,  $n_1 = 6$ ,  $n_2 = 6$ ,  $u = 3$ ,  $P < 0.05$ ). Because the temporal change in both fledgling sex ratio and jack rabbit density suggested some manner of periodicity (Fig. 1), we determined (Bulmer 1974: appendix I) whether variation in fledgling sex ratio was independent of jack rabbit density.

Sine curves with a periodicity of 10 yr, based on maximum jack rabbit density values in 1971 and 1981, provided adequate fits to both sex ratio ( $r^2 = 0.509$ ,  $P = 0.041$ ) and jack rabbit density ( $r^2 = 0.664$ ,  $P = 0.004$ ) curves. Mean ( $\pm$ SE) values about which the curves oscillated were  $25.72 \pm 6.52$  and  $1.89 \pm 0.08$  for jack rabbit density (No./km<sup>2</sup>) and fledgling sex ratio (males: females), respectively. The difference between the 2 curves (jack rabbit - sex ratio) was not significant ( $z = 0.567$ ,  $P = 0.570$ ), indicating that fledgling sex ratio was highly correlated with jack rabbit density.

The close fit between the jack rabbit densities and sex ratios curves provides only partial support of Edwards and Collopy's (1983) suggestion that the increased probability for siblicide occurrence in F-M broods could affect fledgling sex ratios during periods of decreased food availability. The general trend in sex ratio corresponded with jack rabbit density, but few of the yearly sex ratios deviated statistically from 1:1. Rather than the predicted shift from an even to a female-biased sex ratio, decreased food availability appeared to shift a male-biased sex ratio towards an even ratio. Thus, shifts in sex ratio were in the appropriate direction with respect to food availability (i.e. more females than males reach fledging), but were not of the magnitude predicted.

The consistent male bias is somewhat surprising because female Golden Eagles and females of other sexually dimorphic raptors usually suffer greater postfledging mortality than males (Newton 1979, Bortolotti 1986). If females suffer greater postfledging mortality, then population level sex ratios of breeding adults at BOPA should be skewed even more in favor of males. One consequence of male bias would be increased opportunities for subadult females to find vacant breeding slots. Breeding by subadult males should be relatively rare. Although sample size was small, only 2 of 6 known-sex breeding attempts by subadult eagles in BOPA from 1970-1981 were female (Steenhof et al. 1983). This suggests males are not over-represented in the breeding population, and that subadult males either have lower survivorship relative to females or have greater dispersal tendencies.

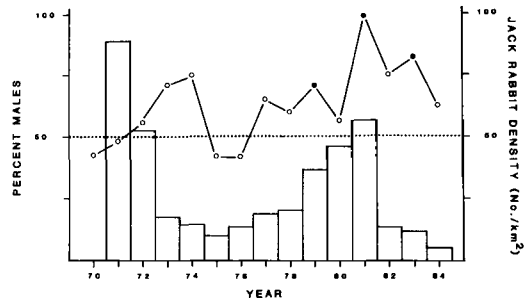


Fig. 1. Change in Golden Eagle fledgling sex ratio plotted as percentage males (circles) and black-tailed jack rabbit density (histograms) from 1970-1984, Snake River Birds of Prey Area, Idaho. Because jack rabbit density was not estimated in 1972, the 1972 value is the midpoint between 1971 and 1973. Solid circles represent SDs ( $P < 0.05$ ) from a 1:1 sex ratio.

Additional work on postfledging mortality and dispersal patterns of young is needed.

It has been suggested that females can manipulate hatching sequence during periods of low prey abundance and establish a situation whereby siblicide could occur easily (Edwards and Collopy 1983, Bortolotti 1986), but the more likely explanation is that F-M hatching sequences occur randomly (Ankney 1982, Cooke and Harmsen 1983, Ryder and Termaat 1987). Manipulation of offspring sex and hatching sequence by female Golden Eagles would require a physiological mechanism that allocates sex chromosomes non-randomly. The existence of such a mechanism in birds is unknown. The strong correspondence between the sex ratio and jack rabbit abundance does not require active manipulation of offspring sex and hatching sequence by females. Rather, the increased likelihood of siblicidal brood reduction in randomly occurring F-M Golden Eagle broods decreases the male bias in fledgling sex ratios during periods of low food availability.

We thank A. R. Bammann, J. H. Doremus, and the numerous technicians who assisted in field data collection. H. D. Bradshaw, R. J. Pierotti, W. Richter and S. A. Temple made helpful comments on this and earlier drafts. This paper is a contribution of the Bureau of Land Management's Snake River Birds of Prey Research Project, and is paper No. 9022 of the Florida Agricultural Experiment Station, Gainesville, Florida.

#### LITERATURE CITED

- ANKNEY, C. D. 1982. Sex ratio varies with egg sequence in Lesser Snow Geese. *Auk* 99: 662-666.
- BORTOLOTTI, G. R. 1986. Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* 127: 495-507.
- BULMER, M. G. 1974. A statistical analysis of the 10-year cycle in Canada. *J. Anim. Ecol.* 43: 701-718.

- COOKE, F., & R. HARMSSEN. 1983. Does sex ratio vary with egg sequence in Lesser Snow Geese? *Auk* 100: 215-217.
- EDWARDS, T. C., JR., & M. W. COLLOPY. 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* 100: 630-635.
- , & M. N. KOCHERT. 1986. Use of body weight and length of footpad as predictors of sex in Golden Eagles. *J. Field Ornithol.* 57: 317-319.
- GARGETT, V. 1977. Sibling aggression in the Black Eagle in the Matapos, Rhodesia. *Ostrich* 49: 57-63.
- MOCK, D. W. 1984. Infanticide, siblicide, and avian nestling mortality. Pp. 3-30 in *Infanticide: comparative and evolutionary perspectives* (G. Hausfauter and S. B. Hrdy, Eds.). New York, Aldine.
- . 1985. Siblicidal brood reduction: the prey size hypothesis. *Am. Nat.* 125: 327-343.
- NEWTON, I. 1979. Population ecology of raptors. Vermillion, South Dakota, Buteo Books.
- RYDER, J. P., & B. M. TERMAAT. 1987. Secondary sex ratios and egg sequence in Herring Gulls. *Auk* 104: 526-528.
- SAFRIEL, U. N. 1981. Social hierarchy among siblings in broods of the Oystercatcher *Haematopus ostralegus*. *Behav. Ecol. Sociobiol.* 9: 59-63.
- SMITH, G. W., & N. C. NYDEGGER. 1985. A spotlight line-transect method for surveying jack rabbits. *J. Wildl. Manage.* 49: 699-702.
- SOKAL, R. R., & F. J. ROHLF. 1981. *Biometry*, 2nd ed. New York, W. H. Freeman and Co.
- SPELLERBERG, I. F. 1971. Breeding behaviour of the McCormick Skua *Catharacta maccormicki* in Antarctica. *Ardea* 59: 189-230.
- STEENHOF, K. 1987. Assessing raptor reproductive success and productivity. Pp. 157-170 in *Raptor management techniques manual* (B. A. Giron Pendelton, B. A. Millsap, K. W. Kline, and D. M. Bird, Eds.). Washington, D.C., Nat. Wildl. Fed.
- , & M. N. KOCHERT. 1982. An evaluation of methods used to estimate raptor nesting success. *J. Wildl. Manage.* 46: 885-893.
- , ———, & J. H. DOREMUS. 1983. Nesting of subadult Golden Eagles in southwestern Idaho. *Auk* 100: 743-747.
- U.S. DEPARTMENT OF INTERIOR. 1979. Snake River birds of prey special research report. Bureau of Land Manage. Boise District, Idaho.
- WERSCHKUL, D. F. 1979. Nestling mortality and the adaptive significance of early locomotion in the Little Blue Heron. *Auk* 96: 116-130.
- WILLIAMS, D. A. 1976. Improved likelihood ratio tests for complete contingency tables. *Biometrika* 63: 33-37.

Received 26 January 1988, accepted 8 June 1988.

### Soil Analyses and $^{13}\text{C}/^{12}\text{C}$ Ratios Identify Sites of Deserted Rockhopper Penguin Colonies

P. J. MOORS,<sup>1</sup> T. W. SPEIR,<sup>2</sup> AND G. L. LYON<sup>3</sup>

<sup>1</sup>Science Directorate, Department of Conservation, P.O. Box 10-420, Wellington, New Zealand,

<sup>2</sup>New Zealand Soil Bureau, Private Bag, Lower Hutt, New Zealand, and

<sup>3</sup>Institute of Nuclear Sciences, Department of Scientific and Industrial Research, Private Bag, Lower Hutt, New Zealand

During the 1940s the breeding population of Rockhopper Penguins (*Eudyptes chrysocome*) at Campbell Island (52°33'S, 169°09'E), in the Australasian quadrant of the Southern Ocean, probably exceeded a million birds (Bailey and Sorensen 1962, Moors 1986). Since then, numbers have fallen dramatically. Breeding colonies have been deserted and the remainder are now greatly reduced in area and numbers of occupants (Moors 1986). Seas around the island have warmed over the past 40 years (Moors unpubl. data), and the consequent change in food availability is the most likely cause of the decline.

Comparisons of present numbers with field observations and photographs taken intermittently between 1941 and the early 1950s were used to assess the extent of this decline. Such evidence is, however, inadequate or absent for several colonies. We inves-

tigated the use of chemical analyses of soil to identify deserted breeding sites of the Rockhopper Penguin.

Rockhopper colonies on Campbell Island are generally on rocky slopes close to the sea. The same breeding locations are used each year, and birds are present from mid-October through the end of April. A breeding Rockhopper Penguin produces 4.3-36.3 g dry wt of guano each day. The excreta contain high concentrations of nitrogen, phosphorus, calcium, and other elements (Burger et al. 1978). Colonies often contain thousands of breeding birds and the underlying soil becomes heavily enriched by their guano. Lower amounts of nutrients are also deposited from molted feathers and the decomposed remains of eggs, dead birds, and food (Williams and Berruti 1978, Siegfried et al. 1978, Williams et al. 1978).

Rockhopper Penguins feed entirely at sea, and the