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LITERATURE CITED

- ASCHOFF, J., & H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körperlänge. *J. Ornithol.* 3: 38-47.
- BAUDINETTE, R. V., & K. SCHMIDT-NIELSEN. 1974. Energy cost of gliding flight in Herring Gulls. *Nature* 248: 83-84.
- BENT, A. C. 1937. Life histories of North American birds of prey. *Bull. U.S. Natl. Mus.* 167: 69.
- BERGER, M., & J. S. HART. 1974. Physiology and energetics of flight. Pp. 416-477 in *Avian biology*, vol. 4 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology. Pp. 77-128 in *Avian biology*, vol. 5 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- BLEM, C. R. 1980. The energetics of migration. Pp. 175-224 in *Animal migration, orientation and navigation* (S. A. Gauthreaux, Jr., Ed.). New York, Academic Press.
- BROWNING, M. R. 1974. Comments on the winter distribution of the Swainson's Hawk (*Buteo swainsoni*) in North America. *Amer. Birds* 28: 865-867.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4-70 in *Avian energetics* (R. A. Paynter, Jr., Ed.). Cambridge, Massachusetts, Nuttall Ornithol. Club.
- LASIEWSKI, R. C., & W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23.
- LASLEY, G. W., & C. SEXTON. 1985. South Texas region. *Amer. Birds* 39: 75-77.
- NEWTON, I. 1979. Population ecology of raptors. Berkhamsted, England, T. & A.D. Poyser.
- NISBET, I. C. T. 1963. Weight loss during migration. Part II: Review of other estimates. *Bird-Banding* 34: 139-159.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. *Ibis* 111: 525-556.
- . 1972. *Animal flight*. Inst. Biol. Studies in Biol., No. 33. London, Edward Arnold.
- . 1975. Mechanics of flight. Pp. 1-75 in *Avian biology* (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- ROGERS, D. T., & E. P. ODUM. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. *Wilson Bull.* 78: 415-433.
- SMITH, N. G. 1980. Hawk and vulture migrations in the Neotropics. Pp. 51-65 in *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation* (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.
- . 1985a. Dynamics of the transisthmian migration of raptors between Central and South America. Pp. 271-290 in *Conservation studies on raptors*, ICBP Tech. Publ. No. 5 (I. Newton and R. D. Chancellor, Eds.). London, Intern. Council for Bird Protection.
- . 1985b. Some uncertain aspects of migration by Swainson's Hawks (*Buteo swainsoni*) and Turkey Vultures (*Cathartes aura*). Rochester, New York, Proc. North American Hawk Migration Conf. No. 4.
- . 1985c. Thermals, cloud streets, trade winds, and tropical storms: how migrating raptors make the most of atmospheric energy in Central America. Rochester, New York, Proc. North American Hawk Migration Conf. No. 4.
- TUCKER, V. A. 1971. Flight energetics in birds. *Amer. Zool.* 11: 115-124.
- WEIS-FOGH, T. 1952. Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forshal). *Phil. Trans. Royal Soc. London, Ser. B* 237: 1-36.

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The First Documented Case of Polyandry for Wilson's Phalarope (*Phalaropus tricolor*)

MARK A. COLWELL

Biology Department, University of North Dakota, Grand Forks, North Dakota 58202 USA

Phalaropes are noted for their unusual mating system in which males provide all parental care and females compete for mates (Oring 1982). This reversal of the sex roles is characteristic of classical polyandry, a rare mating system among birds (Oring 1985). Despite evidence that phalaropes exhibit sex-role reversal and polyandry (Oring 1982), sequential poly-

andry was proven only recently for Red-necked (*Phalaropus lobatus*; Hildén and Vuolanto 1972, Reynolds et al. 1985) and Red phalaropes (*P. fulicaria*; Schamel and Tracy 1977). I present here the first documented case of polyandry for Wilson's Phalarope (*P. tricolor*).

I studied Wilson's Phalaropes from 1982 to 1985

near the northern extreme of their range at Last Mountain Lake Wildlife Management Unit in south-central Saskatchewan (Reynolds et al. 1985). Each year I began research upon arrival of phalaropes in early May and continued until 31 July. I marked each bird with a unique combination of 3 colored leg bands and an aluminum band. In 1984 and 1985, I also marked individuals with a patagial tag. Over the 4 years I marked 69 females (8 in 1982, 6 in 1983, 32 in 1984, 23 in 1985), but recorded polyandry only in 1985. However, many of the females were marked late in the breeding season; thus, these numbers may not accurately portray the incidence of polyandry in this population.

In 1985, I located 63% (51 of 81) of all nests during the laying stage and banded 9 females while they were laying in known nests during the first 2 weeks of the nesting period (14–27 May). All 9 females courted additional males following completion of their first clutches. One of these females also briefly, but repeatedly, associated with the male incubating her first clutch. Of these 9 females, 8 left the study area within a week of being banded. I do not know whether these females successfully obtained additional mates. One female remained in the study area and acquired a second mate. Female BA:YY was netted on 16 May. During the morning of 17 May I found her 1-egg clutch, the second phalarope clutch of the season to be initiated in the area. She laid a second egg at 1230 the same day. Her mate (YdG:AR) was caught and banded on 18 May. The clutch was completed on 19 May. Shortly after completing her first clutch, BA:YY began courting additional males. On 28 May I banded a male (YR:RA). I observed YR:RA copulating with BA:YY on 29 May, and a day later found their 2-egg clutch. BA:YY finished laying for YR:RA on 1 June and again began courting males. I last saw her on 14 June, approximately 10 days before the last phalarope clutch was initiated in the study area.

In a year when the population sex ratio of Red-necked Phalaropes was slightly male-biased, the first two females to complete nesting obtained second mates (Hildén and Vuolanto 1972). The population

sex ratio at Last Mountain Lake was not known; however, a male-biased sex ratio is not necessary for polyandry to occur, at least among phalaropes. All that is required is for early-nesting females to re-enter the breeding population and successfully compete for males (Emlen and Oring 1977). I suspect polyandry is more common among Wilson's Phalaropes than this single case suggests. Detection of polyandry is hampered, however, by movement of females following completion of their first clutch.

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LITERATURE CITED

- EMLEN, S. T., & L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197: 215–223.
- HILDÉN, O., & S. VUOLANTO. 1972. Breeding biology of the Red-necked Phalarope, *Phalaropus lobatus*, in Finland. *Ornis Fennica* 49: 129–144.
- ORING, L. W. 1982. Avian mating systems. Pp. 1–92 in *Avian biology*, vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- . 1985. Avian polyandry. Pp. 309–351 in *Current ornithology*, vol. 3 (R. F. Johnston, Ed.). New York, Academic Press.
- REYNOLDS, J. D., M. A. COLWELL, & F. COOKE. 1986. Sexual selection and spring arrival times of Red-necked and Wilson's phalaropes. *Behav. Ecol. Sociobiol.* in press.
- SCHAMEL, D., & D. TRACY. 1977. Polyandry, replacement clutches, and site tenacity in the Red Phalarope (*Phalaropus fulicarius*) at Barrow, Alaska. *Bird-Banding* 48: 314–324.

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