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Warren, S.M., Fox, A.D., Walsh, A. & O'Sullivan, P. (1993)

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relation to the lunar cycle. Ornis Scand. 21:147–156. ·

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. SPSS statistical package for the social sciences. McGraw-Hill, New York.

PETTIGREW, J. D., AND B. J. FROST. 1985. A tactile fovea in the Scolopacidae? Brain Behav. Evol. 26:185–195.

PIENKOWSKI, M. W. 1981. How foraging plovers cope with environmental effects on invertebrate behaviour and availability. Pages 179–182 *in* Feeding and survival strategies of estuarine organisms (N. V. Jones and W. J. Wolff, Eds.). Plenum Press, New York.

PIENKOWSKI, M. W. 1982. Diet and energy intake of Grey and Ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. J. Zool. (Lond.) 197:511–549.

PIENKOWSKI, M. W. 1983a. Changes in the foraging pattern of plovers in relation to environmental factors. Anim. Behav. 31:244–264.

PIENKOWSKI, M. W. 1983b. Surface activity of some intertidal invertebrates in relation to temperature and foraging behaviour of their shorebird predators. Mar. Ecol. Prog. Ser. 11:141–150.

ROBERT, M., AND R. MCNEIL. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. Ibis 131:69–79.

ROBERT, M., R. MCNEIL, AND A. LEDUC. 1989. Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. Auk 101:94–101.

ROCHON-DUVIGNEAUD, A. 1943. Les yeux et la vision des vertébrés. Masson et Cie, Paris.

ROJAS DE AZUAJE, L. M. 1991. Proporción de conos y bastones en la retina de tres especies de aves limícolas y la relación entre visión y estrategia alimenticia. Tesis de M.Sc., Instituto de Investigaciones en Biomedicina y Ciencias Aplicadas, Univ. Oriente, Cumaná, Venezuela.

SCHNEIDER, D. C. 1983. The food and feeding of migratory shorebirds. Oceanus 26:38–43.

SCHWARTZKOPFF, J. 1973. Mechanoreception. Pages 417–477 *in* Avian biology, vol. 3 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

SPENCER, K. G. 1953. The Lapwing in Britain. A. Brown & Sons, London.

SUTHERLAND, E. J. 1982. Do oystercatchers select the most profitable cockles? Anim. Behav. 30:857–861.

TANSLEY, K., AND J. T. ERICHSEN. 1985. Vision. Pages 623–629 *in* A dictionary of birds (B. Campbell and E. Lack, Eds.). Poyser, Calton, United Kingdom.

VAN HEEZIK, Y. M., A. F. C. GERRITSEN, AND C. SWENNEN. 1983. The influence of chemoreception on the foraging behaviour of two species of sandpiper, *Calidris alba* and *Calidris alpina*. Neth. J. Sea Res. 17:47–56.

VON BOLZE, G. 1968. Anordnung und Bau der herbstschen Köperchen in Limicolenschnäbeln im Zusammenhang mit der Nahrungsfindung. Zool. Anz. 181:313–343.

WALLS, G. L. 1942. The vertebrate eye and its adaptive radiation. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Extended Parent-Offspring Relationships in Greenland White-fronted Geese (*Anser albifrons flavirostris*)

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Continuing associations between parents and fledged offspring are uncommon among most bird species. They are, however, especially prevalent in territorial species with cooperative breeding (see Brown 1987). Although cooperative breeding has not been recorded in wildfowl, it has long been recognized that juvenile geese remain with their parents for at least part of their first year (Phillips 1916, Elder and Elder 1949, Hochbaum 1955). Guiding offspring on migration to traditional staging and wintering sites and teaching offspring valuable foraging techniques and social skills, as well as the locations of safe and productive feeding and roosting sites, are common explanations for the prolonged parent–offspring relationships in migratory geese and swans.

Greenland White-fronted Geese (*Anser albifrons flavirostris*; Dalgety and Scott 1948) breed in West Greenland between 64° and 72°N, and winter exclusively
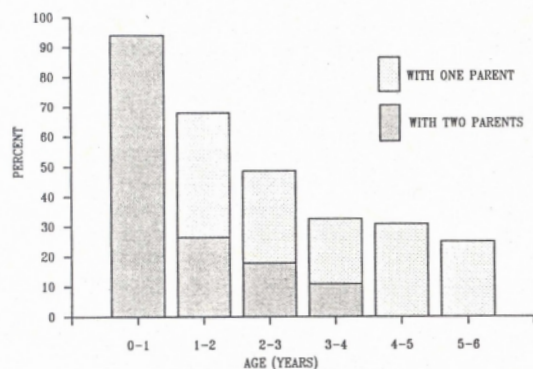
Fig. 1. Longevity of parent–offspring relationships in Greenland White-fronted Geese banded at Wexford, Ireland.

in Ireland, Scotland and Wales. In the 1970s, the population had declined to between 14,300 and 16,600 due mainly to the loss of bog-land habitat traditionally used by the geese (Ruttledge and Ogilvie 1979). By November 1989 the population had recovered to 27,000 individuals, the increase being due to protective legislation and conservation measures on the breeding and wintering grounds (Wilson et al. 1991). However, there is still continued concern for the well being of the population. The Irish National Parks and Wildlife Service initiated a marking/resighting scheme in 1982 with the aim of understanding better the site movements, habitat use and social behavior of geese, leading to improved management of the population. This paper reports on the findings of a detailed analysis of the resighting data of geese of known age with respect to the persistence of parent–offspring relationships.

Geese were cannon netted at Wexford, Co. Wexford, Ireland between October and December. They were marked with standard metal bands and individually coded plastic leg bands and neck collars. Geese were sexed by cloacal examination, aged on plumage characteristics as juveniles (<1 year) or adults, and weighed and measured. Birds were retained in holding pens before being released together to avoid break-up of family units.

As of March 1991, 843 geese were marked, 790 on the Wexford Slobs (where more than one-half of the population winters) and 53 elsewhere in Ireland. More than 15,800 resightings of individually marked birds have been made, the majority of which yield information on the social status of marked birds and their associates.

Three or four days each week from late September to April were spent "resighting" individually marked geese on the North and South Slobs at Wexford. The Wexford Slobs are intensively farmed lands, reclaimed from Wexford Harbour in the middle of the last century. Observers drove a regular network of roads throughout the Slobs and observed the geese,

without disturbing them, using telescopes ($60\times$ magnification allows collars to be read as far as 800 m away). The other Irish and Scottish sites that are used by White-fronted Geese were also covered on a regular basis. When a marked bird was resighted, the status of the bird (i.e. paired, unpaired, with adults or juveniles) was determined and the number of associated geese recorded (i.e. presence of mate and number of parents, siblings or goslings). The band numbers of associated marked geese were recorded, when possible; otherwise, associates were termed as "unbanded."

Definitive family relationships (parent–offspring and sibling–sibling associations) were determined for juveniles in their first winter. Only those birds that had two banded parents were used in the subsequent analysis. The number of these geese associated each winter with one, two, or no parents was determined and expressed as a proportion of the total number of marked geese seen of that age. The social status of those geese that were with neither parent also was determined (i.e. whether paired, associated with siblings, or loosely associated with other geese of unknown relatedness). Of the 383 juvenile White-fronted Geese banded in Ireland, 188 had both parents banded and were used in the analysis. Parent–offspring cohesion was extensive (Fig. 1).

In their first winter (i.e. at three to nine months of age), juveniles were associated with one or more parents on 94.0% of occasions ($n = 188$ birds) and family cohesion was consistent throughout the winter. When birds were recorded without parents (on odd occasions), they were usually associated with a sibling. There were only two records of banded orphans in their first year (omitted from analysis). The family status of birds in subsequent (i.e. second to sixth) winters is shown in Table 1.

The mean age for males leaving the family was 1.65 ± SE of 0.139 years ($n = 34$), whereas the mean age for females leaving the family was 2.00 ± 0.183 years ($n = 21$). However, this difference is nonsignificant (Mann-Whitney $W = 864.5$, $P = 0.132$).

No evidence suggested that geese left their families when their parents bred again. Five banded pairs bred in consecutive years and, in four of these, at least one of the brood was banded and was still associated with its parents and the new brood in the following year.

As most families contained more than one bird banded as a juvenile, it was possible to identify sibling attachments once geese had left their parents. On average, 13.8% of birds were associated with one or more sibling after having left their parents. Also, each year 11% of geese paired upon leaving, and 14% were associated with geese outside the family.

The common explanations for extended parental care in geese and swans are also attributable to Greenland White-fronted Geese. However, they do not explain the extreme longevity of the relationships found in this analysis. A combination of (1) large body size

TABLE 1. Family status of Greenland White-fronted Geese banded in Ireland as juveniles in winters following banding. Data shown as number of geese seen with one, two or no parents, and as a percentage (in parentheses) of number of banded geese (of that age class) seen in that winter.

Seen with	Winter				
	Second	Third	Fourth	Fifth	Sixth
Two parents	52 (41.6)	24 (30.8)	10 (21.7)	—	—
One parent	33 (26.4)	14 (17.9)	5 (10.9)	4 (30.8)	2 (25.0)
No parents	35 (28.0)	33 (42.3)	30 (65.2)	6 (46.1)	6 (75.0)
Unknown	5 (4.0)	7 (9.0)	1 (2.2)	3 (23.1)	—
Total	125	78	46	13	8

and how this relates to flock behavior and feeding ecology, (2) the highly scattered and remote distribution of traditional wintering sites, and (3) the possible existence of alloparental care (Ely 1979, Stroud *in* Fox and Stroud 1981) may explain to some extent the extreme persistence of parent–offspring associations in this species.

Greenland White-fronted Geese are relatively large and traditionally feed on highly nutritious bog plants (Ruttledge 1929, Fox et al. 1990). They are also notable for being the least gregarious of British geese. It appears that there are fewer requirements among such species to form large, highly dense flocks and, hence, family associations are easily maintained. This hypothesis explains why larger goose species, such as the Giant Canada Goose (*Branta canadensis maxima*; Raveling 1979), appear to have longer parent–offspring relationships than the highly gregarious small goose species, such as the Cackling Canada Goose (*B. c. minima*; Johnson and Raveling 1988) and Ross's Goose (*Anser rossi*; McLandress *in* Johnson and Raveling 1988), which primarily graze on low-quality grasslands in large aggregations.

Greenland White-fronted Geese traditionally wintered on lowland peatlands, and a proportion of the population still depends on these traditional sites. The geese are extremely site loyal, often returning to the same bog (or field, in more recent times) each winter (Wilson et al. 1991, Warren et al. 1992). "Teaching" offspring to locate these often scattered and remote feeding sites almost certainly has been an important factor in the evolution of this unusual social behavior. Bewick's Swans (*Cygnus columbianus bewickii*) also are traditionally site faithful (Scott 1978) and have long-term family ties (Scott 1980). Retaining the family unit, along with extreme site loyalty, has all the advantages of flocking (such as shared vigilance; Lazarus 1978), but individuals share the costs and benefits with their own kin rather than unrelated birds. Although teaching offspring the locations of traditional wintering sites is likely to have been an important factor in the evolution of this behavior, more than one-half of the population currently winters on a relatively small area of intensively farmed grassland. Hence, this behavior may now be somewhat obsolescent.

Yearling Greenland White-fronted Geese have been seen on the breeding grounds associating with adult geese (presumably their parents) at the nest and with their parents' newly hatched goslings (Stroud *in* Fox and Stroud 1981). Nest attendance and nest defense by yearling Pacific White-fronted Geese (*Anser albifrons frontalis*) also has been documented (Ely 1979). Attendance at their parents' nest and the defensive behavior of offspring from previous years may well be a form of alloparental care. This behavior may be particularly important in Greenland White-fronted Geese as nest predation is high (Fox and Stroud 1988), and very few pairs succeed in returning to the wintering grounds with young (Fox et al. 1983).

LITERATURE CITED

BROWN, J. L. 1987. Helping and communal breeding in birds. Princeton Univ. Press, Princeton, New Jersey.

DALGETY, C. T., AND P. SCOTT. 1948. A new race of the White-fronted Goose. Bull. Br. Ornithol. Club. 68:109–121.

ELDER, W. H., AND N. L. ELDER. 1949. Role of the family in the formation of goose flocks. Wilson Bull. 61:133–140.

ELY, C. R. Breeding biology of the White-fronted Goose. M.S. thesis, Univ. California, Davis.

FOX, A. D., AND D. A. STROUD (EDS.). 1981. Report of the 1979 Greenland White-fronted Goose Study Expedition to Eqalungmiut Nunaat, West Greenland. Greenland White-fronted Goose Study, Aberystwyth, Wales.

FOX, A. D., AND D. A. STROUD. 1988. The breeding biology of the Greenland White-fronted Goose. Meddelelser om Grønland. BioScience 27:1–16.

Fox, A. D., J. Madsen, and D. A. Stroud. 1983. The summer ecology of the Greenland White-fronted Goose *Anser albifrons flavirostris*. Dan. Ornithol. Foren. Tidsskr. 77:43–55.

Fox, A. D., D. A. Stroud, and I. S. Francis. 1990. Up-rooted common cotton grass *Eriophorum angustifolium* as evidence of goose feeding in Britain and Ireland. Bird Study 37:210–212.

Hochbaum, H. A. 1955. Travels and traditions of waterfowl. Univ. Minnesota Press, Minneapolis.

Johnson, J. C., and D. G. Raveling. 1988. Weak family associations in Cackling Canada geese during winter: Effects of size and food resources on goose social organization. Pages 71–89 *in* Waterfowl in winter (M. Weller, Ed.). Univ. Minnesota Press, Minneapolis.

Lazarus, J. 1978. Vigilance, flock size and domain of danger in the White-fronted Goose. Wildfowl 29:135–145.

Phillips, J. C. 1916. Behavior and make up of the migratory flocks of Canada Geese. Auk 33:24–27.

Raveling, D. G 1979. Traditional use of migration and winter roost sites by Canada Geese. J. Wildl. Manage. 43:229–235.

Ruttledge, R. F. 1929. The birds of Loughs Mask

and Carra and surrounding district. Ir. Nat. J. 11: 223.

Ruttledge, R. F., and M. A. Ogilvie. 1979. The past and current status of the Greenland White-fronted Goose in Ireland and Britain. Ir. Birds 1:293–363.

Scott, D. K. 1978. Social behaviour of wintering Bewick's Swans. Ph.D. thesis, Univ. Cambridge, Cambridge.

Scott, D. K. 1980. Functional aspects of prolonged parental care in Bewick's Swans. Anim. Behav. 28:938–952.

Warren, S. M., A. D. Fox, A. J. Walsh, O. J. Merne, and H. J. Wilson. 1992. Wintering site interchange amongst Greenland White-fronted Geese *Anser albifrons flavirostris* captured at Wexford Slobs, Ireland. Bird Study. In press.

Wilson, H. J., D. W. Norriss, A. Walsh, A. D. Fox, and D. A. Stroud. 1991. Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*: Implications for conservation and management. Ardea 79:287–294.

Intergradation Between the Bush-Tanagers
Chlorospingus punctulatus and *C. ophthalmicus* in Western Panama
(Aves: Thraupidae)

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The taxa included under *Chlorospingus ophthalmicus* (Common Bush-Tanager) show complex geographic variation throughout the vast range of the species from Mexico to Argentina. For example, there are 10 named subspecies divided into at least 14 discrete populations in Colombia and Venezuela alone (Olson 1983). Three taxa in this complex have been named from western Panama. One of these, *C. punctulatus* Sclater and Salvin 1869, found in the provinces of Veraguas and Coclé (Fig. 1), is sufficiently distinct from the others in its very dark cap and more intense coloration that it has almost always been given the status of a separate species (e.g. Hellmayr 1936 [and all previous authors], Eisenmann 1955, Storer 1970), or has been maintained as its own subspecies "group" (AOU 1983).

The subspecies *C. o. regionalis* Bangs 1906 ranges from the mountains of Costa Rica to the western slope of the Volcán de Chiriquí in Panama. Although its distribution had previously been misunderstood, the

population known as *C. o. novicius* Bangs 1902 was shown to occur (Olson 1981) only on the eastern slope of Volcán de Chiriquí (Fig. 1), mainly in the vicinity of the town of Boquete. This form is decidedly more richly colored than *C. o. regionalis* and was considered to show some approach to the coloration of *C. punctulatus* (Olson 1981).

These bush-tanagers are common and conspicuous where they occur and the absence of specimens between western Chiriquí and central Veraguas is probably an artifact of collecting due to lack of roads in the mountains in the area. Construction of an oil pipeline and an accompanying highway (often known as the Fortuna or *"oleoducto"* road; Ridgely and Gwynne 1989), from Gualaca on the Pacific slope of Chiriquí to Chiriquí Grande on the Caribbean slope of Bocas del Toro, provided access to mountainous habitats some 25 km east of the Boquete area. Birds of the *C. ophthalmicus* complex were observed along this road and referred to the subspecies *novicius* by Ridgely and