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FAMILY STABILITY IN GREATER WHITE-FRONTED GEESE

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ABSTRACT.—I investigated the stability of parent–offspring bonds, and sibling–sibling bonds of neck-banded Greater White-fronted Geese (*Anser albifrons frontalis*) during winters (September–May) in California and southern Oregon from 1979 to 1989. Geese captured at feeding sites were more likely to be in social groups than those captured at roosting sites. Offspring remained associated with their parents longer than reported for other geese, as 69% of yearlings, 39% of two-year-olds, and 38% of three-year-olds and older were observed with their parents during winter. The proportion of time offspring spent with their parents declined as they grew older, being 76% for juveniles, 32% for yearlings, and 15% for two-year-olds and older. The prevalence of extended family groups was corroborated by counts of landing groups of unmarked geese. Sibling bonds also persisted after the first year of life, with 74%, 50%, and 39% of siblings maintaining some degree of social contact at ages of one, two and three years or older, respectively. Older offspring were more likely to associate with brood mates than with parents. Intensive observations ended when the oldest known-age geese were 34 months old. Incidental sightings in subsequent years revealed that some offspring up to eight years of age still associated with their parents and/or siblings. The benefits of maintaining long-term family bonds were not readily apparent, as there was no difference in the reproductive success of parents with and without attendant offspring, and yearlings that associated with parents were not more likely to survive than yearlings that did not associate with parents. However, older offspring and their parents may benefit by remaining together if extended families are more dominant and have better access to limited food and safe roost sites. Parents benefit if their fitness is enhanced due to nest defense provided by older offspring, and subadults probably benefit from staying with their parents by learning foraging and predator avoidance strategies from parents and older siblings.
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PROLONGED PARENT–OFFSPRING bonds, and extended family groups, although well documented in sedentary bird species (Brown 1987), are uncommon in migrant species (Wittenberger 1981:99). This is due in part to the greater difficulty of maintaining social ties during migration (Rowley 1983), and the temporal and energetic constraints placed on the social behavior of migratory waterfowl (Kear 1970). Geese (tribe Anserini), in particular, have evolved a complexity of behaviors that promote family and pair-bond cohesiveness, including the triumph ceremony (Fischer 1965), preflight signalling (Raveling 1969a, Black and Barrow 1985), and formation flying (Gould and Heppner 1974), but only rarely have offspring of geese been reported to remain with their family be-

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FRONTISPIECE. Extended family group of Greater White-fronted Geese (*Anser albifrons frontalis*) landing in a grain field in the Klamath Basin, California. Painting by K. Williams-Holyfield.

yond their first year (Boyd 1959, Raveling 1969b, Prevett and MacInnes 1980, Warren et al. 1992). Most commonly juvenile geese become independent either during autumn or winter (Jones and Jones 1966, Johnson and Raveling 1988, Black and Owen 1989a), or during spring or summer when they are expelled by the gander (Fischer 1965, Prevett and MacInnes 1980, Dittami 1981, Gautier and Tardif 1991).

Here I present detailed information on the integrity of parent-offspring and sibling-sibling bonds in Greater White-fronted Geese (*Anser albifrons frontalis*; see frontispiece) obtained during more than three years (1979–1982) of intensive observation of individually marked birds wintering in California and southern Oregon. I show the existence of persistent parent-offspring and sibling bonds, which has important implications in understanding the structure of goose populations and factors controlling and contributing to survival and fitness. While there has long been an appreciation for the complex social system of geese, much of what is known has been based on observations of captive or semicaptive geese (Lorenz 1966). My study of wild geese reveals an even more elaborate social structure than previously recognized.

METHODS

The study was conducted in southern Oregon and northern California, the major wintering area of this species in the Pacific Flyway. Fieldwork took place from October through April 1979–1980, and September through April during 1980–1981, and 1981–1982. Additional observations were made opportunistically through October 1989.

Marking.—Geese were captured with propelled nets in California during autumn, winter, and spring 1979–1981, and by driving flightless geese in Alaska during July 1981. Geese were fitted with coded plastic neck collars and metal U.S. Fish and Wildlife Service leg bands (Ely 1990). All geese captured at the same time were released as a group to decrease the likelihood of separating families (Miller and Dzubin 1965). Age (adult or juvenile) was determined based on plumage (Boyd 1953), and sex determined by cloacal examination (Owen 1980).

Geese at wintering areas were captured at roost sites, and at feeding sites in agricultural fields. Determination of the influence of marking on social group separation is restricted to geese marked and reobserved in the Klamath Basin, California, as samples elsewhere were small, and there was a reduced probability of resighting geese outside the Klamath Basin.

Social classes.—Four social classes of geese were recognized: (1) pair refers to adult geese obviously associated with each other based on behavior (Fischer 1965), or repeated sightings in close proximity; (2) single is used to describe an individual not associated with other geese; (3) family indicates a group comprised of at least one adult-plumaged bird and one juvenile and/or subadult that engaged in a triumph ceremony, acted in unison in aggressive encounters, or were seen together on repeated occasions; (4) sibling group indicates immature geese without associated adults, or same-sex adult-plumaged geese in close association. Marked geese were considered to be "together" during an observation if they maintained proximity to each other throughout the observation period. Greater White-fronted Geese in their second winter (yearlings) and older are indistinguishable from fully mature geese (Owen 1980) and, hence, the status of unmarked adult-plumaged geese could not always be specifically determined. Associations with more than two adult-plumaged geese are referred to as "multiple" adult groups or families.

The proportion of unmarked geese in different social classes was determined by noting the size and age composition of social units of geese as they landed at feeding and roosting sites (Boyd 1959, Lynch and Singleton 1964, Raveling 1968, 1969b). Counts were made throughout the field season, at all localities, to account for temporal and geographic variation.

Observations.—I observed birds from a vehicle during daylight hours while geese fed in agricultural fields or were loafing at roost sites. Most observations were made by four primary observers (1979–1982; author made more than 80%); numerous secondary observers also contributed observations of neck-banded geese.

About 500 (1979–1980) to 1,000 (1980–1981 and 1981–1982) collared geese were available for observation in a given year; some attrition occurred due to mortality and neck-band loss. As there were about 100,000 Greater White-fronted Geese in the Pacific Flyway during the study (U.S. Fish and Wildlife Service unpubl. data), less than 1% of the geese in the population were marked; spurious associations of marked geese, thus, were unlikely.

Status of marked geese.—Assessment of family status was based on observations of geese marked as juveniles and observed on at least two occasions the year of banding with one or more marked adult-plumaged goose. Analyses of the status of known-age geese were restricted to sightings after group members had reunited after banding, and when at least one neck-banded associated goose was also known to be alive, as determined from subsequent observations. Analysis of the proportion of time offspring spent with their parents was restricted to those offspring observed at least five times during a given year.

TABLE 1. Greater White-fronted Geese observed in marked families relative to location and time of banding in Alaska, northern California and southern Oregon during 1979–1982.

Time of banding	Adults			Juveniles		
	No. marked	No. observed	Percent with marked juveniles	No. marked	No. observed	Percent with marked adults
Alaska						
July[a]	176	154	19.5	178	85	36.5
Klamath Basin						
September[a]	32	31	64.5	66	66	74.2
October[a]	248	224	22.3	195	175	30.3
October–November[b]	250	239	15.9	184	169	27.8
Sacramento Valley						
November–January[b]	31	27	37.0	29	27	59.3
Klamath Basin						
March–April[c]	186	174	12.6	35	34	20.6
Total	923	849	20.7	687	556	36.5

[a] Before hunting season.
[b] During hunting season (mid-October to mid-January).
[c] After hunting season.

Neck-banded geese were considered "dead" if reported as such to the banding laboratory or directly to me by hunters, or if a goose did not retain its neck band. The proportion of geese that lost neck bands was determined from hunter questionnaires.

Statistical procedures.—Chi-square tests were used to determine differences in proportion data unless cell sizes were less than five, in which case Fisher's exact test was used (Sokal and Rohlf 1981). Analysis of variance (ANOVA; SAS Institute 1988) was used for evaluating differences among social groups in time to reunite after banding and in mean brood sizes. Among-year variance in the amount of time offspring spent with parents and differences in the proportion of time yearlings and two-year-olds spent with siblings versus parents was tested with the Kruskal-Wallis test (one-way ANOVA applied to ranks; SAS Institute 1988).

RESULTS

Marking.—More than 1,600 geese were captured and fitted with neck bands during the study (Table 1). Geese were marked before (n = 895), during (n = 494), and after (n = 221) the hunting season, which opened in mid-October and closed in mid-January (Table 1).

Proximate factors related to family stability.—Over 24,000 observations were made of collared geese during the study. Most geese marked were observed the year they were captured ($\bar{x}$ = 87% during 1979–1982). Fewer juveniles marked in Alaska were observed than from other marking areas (unpubl. data), and this is reflected in the smaller number of family groups observed containing birds banded in Alaska (see below).

Parents and offspring reunited quickly after they were captured and released; 53% of marked families (n = 64) were back together by the time any members were first observed. The time between release and family reunion ($\bar{x}$ = 5.7 ± SE of 0.9 days) was not significantly related to season of marking (F = 0.21, df = 2 and 62, P = 0.81).

Geese captured before the opening of the hunting season were more likely to be part of family groups than geese caught during or afterward (adults, X^2 = 5.54, df = 1, P = 0.02; juveniles, X^2 = 6.25, df = 1, P = 0.01; Table 1). The difference was largely due to the high proportion of geese in families that were marked during September in the Klamath Basin relative to all other marked samples (adults, X^2 = 5.71, df = 1, P = 0.02; juveniles, X^2 = 46.00, df = 1, $P < 0.001$).

A greater proportion of adult geese captured at field sites were in families than were adult geese caught at roosts during the same time period (31.0% vs. 13.1%; X^2 = 7.40, df = 1, $P <$ 0.01). The same comparison was not significant for juveniles (X^2 = 1.67, df = 1, $P > 0.05$).

Parent–offspring associations.—The proportion of offspring observed with their parents did not vary significantly among years (yearlings, X^2 = 3.77, df = 2, P = 0.15; two-year-olds, X^2 = 4.42,

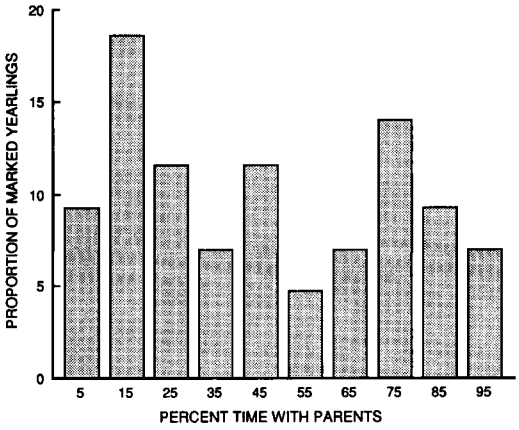

Fig. 1. Distribution of percent time different yearling Greater White-fronted Geese spent with parents (n = 43). Includes only neck-banded yearlings observed more than four times.

df = 2, P = 0.11; three-year-olds, X^2 = 0.68, df = 2, P = 0.71; Table 2), so data were pooled. Parent-offspring associations were prominent throughout the study (Table 2). However, older offspring were less likely to be observed with their parents (X^2 = 16.57, df = 2, P < 0.001; comparing observations of 99 yearlings, 54 two-year-olds, and 29 three-year-olds). Older offspring (≥yearlings) also spent more time away from parents than juveniles (F = 11.19, df = 2 and 95, P = 0.0001; Table 3). The proportion of time different yearlings spent with adults was nearly bimodal in distribution (Fig. 1); some yearlings were nearly always with parents, while others were with parents only infrequently.

In general, yearlings and older offspring were more loosely associated with parents than their younger siblings, and were often on the perimeter of family groups. Older offspring with young occasionally rejoined their parents; the result was several generations of geese acting as a large but loosely associated family.

Although intensive observations ended after the third field season (May 1982), continued observations indicated that parent-offspring bonds persisted after offspring were three years old. Indeed, of the observations of geese 39 months or older, three were of offspring in their eighth year; they were observed with one neck-banded parent at a wintering site in Mexico (R. Drewein and R. Bromley pers. comm.).

There were no significant differences between males and females in the proportion of offspring of each age class associated with parents (yearlings, X^2 = 0.18, df = 1, P = 0.67; two-year-olds, X^2 = 0.51, df = 1, P = 0.48; ≥three-year-olds, X^2 = 2.54, df = 1, P = 0.11; Table 4). The sex ratio of neck-banded geese at the time they were captured was also approximately even (49.8% of 923 adults and 48.9% of 687 juveniles were female).

Approximately 200 (13%) of the 1,610 neck-banded geese in this study were reported shot by hunters during 1979–1982 (unpubl. data). Actual hunting mortality of neck-banded geese is likely much higher, as only a proportion of

TABLE 2. Prevalence of parent-offspring associations in Greater White-fronted Geese relative to age of offspring during winter in southern Oregon and northern California, 1979–1989.[a]

	Age of offspring							
	Juveniles[b]		Yearlings		Two-year-olds		Three-year-olds or older	
Year of banding	No. geese	No. families	No. different geese	Percent with parents	No. different geese	Percent with parents	No. different geese	Percent with parents
1979–1980	58[c]	31	42	69.0 (19[d])	31	38.7 (8)	15	33.3 (4)
1980–1981	76	34	41	61.0 (16)	16	25.0 (4)	8	50.0 (4)
1981–1982	77	30	16[e]	88.4 (7)	7	71.4 (2)	6	33.3 (2)
Total	211	95	99	68.7 (42)	54	38.9 (14)	29	37.9 (10)

[a] Only includes observations of families of neck-banded geese with at least one adult and one offspring known to be alive at time of observation. Offspring considered to be with parents if observed together at least once during the year.

[b] By definition, all juveniles associated with parents.

[c] Includes five juveniles in three families not observed in 1979–1980, but observed following year with parents.

[d] Number of different families.

[e] Includes three yearlings in one family not observed in 1982–1983, but observed with parents in 1983–1984.

TABLE 3. Relationship between age of offspring of Greater White-fronted Geese and proportion of sightings with parents in southern Oregon and northern California, 1979–1989.[a]

Year of banding	Juveniles		Yearlings		Two-year-olds		Three-year-olds or older	
	No. geese	Percent time with parents	No. geese	Percent time with parents	No. geese	Percent time with parents	No. geese	Percent time with parents
1979–1980	43	67.3 ± 4.8	38	31.7 ± 5.2	24	13.7 ± 4.3	7	9.8 ± 5.1
1980–1981	53	75.7 ± 3.6	24	33.0 ± 7.2	2	42.9 ± 42.9	3	24.8 ± 18.1
1981–1982	47	84.3 ± 3.1	—	—	—	—	—	—
Total	143	76.0 ± 2.2	62	32.2 ± 4.2	26	15.9 ± 4.9	10	14.3 ± 6.2

[a] Includes only neck-banded geese observed at least five different times in given year when at least one neck-banded parent also known to be alive at time of observation. $\bar{x}$ ± SE.

banded birds are usually reported to the Bird Banding Office, and unretrieved harvest (injured birds) may be significant (Timm and Dau 1979).

Family groups were observed intact (juveniles with adults) more often before the hunting season ($\bar{x} = 96.92 \pm 2.07$, $n = 12$; if minimum number of sightings of collared juveniles observed before hunting season is lowered from five to four, $\bar{x} = 92.8 \pm 2.6$, $n = 26$) than during ($\bar{x} = 77.05 \pm 2.98$, $n = 67$) or after ($\bar{x} = 67.33 \pm 3.94$, $n = 70$; $F = 8.52$, df = 2 and 16, $P = 0.0003$).

Breakup of families after the hunting season also was indicated by changes in the composition of landing-group counts. The proportion of lone adults with juveniles in landing group counts increased dramatically ($X^2 = 32.48$, df = 1, $P < 0.001$) after the opening of the hunting season, as did the proportion of juveniles in groups without adults ($X^2 = 109.65$, df = 1, $P = 0.001$; Table 5). The number of single adults and juveniles also increased after the opening of the hunting season (lone adults, $X^2 = 33.98$, df = 1, $P < 0.001$; lone juveniles, $X^2 = 109.65$, df = 1, $P > 0.001$).

Landing-group counts revealed that two-adult families and multiple-adult (>2) families contained a similar number of juveniles (two-adult families, $\bar{x} = 2.90 \pm 0.04$, $n = 1{,}442$; >2-adult families, $\bar{x} = 2.70 \pm 0.06$, $n = 545$; $F = 1.42$, df = 1 and 1,969, $P = 0.2335$; controlling for variation among years and season). Broods attended by single adults, however, were significantly smaller than broods attended by more than one adult overall (single-adult broods, $\bar{x} = 2.13 \pm 0.07$, $n = 330$; >1-adult broods, $\bar{x} = 2.85 \pm 0.03$, $n = 1{,}987$; $F = 37.49$, df = 1 and 2,311, $P = 0.001$). Families with only one adult also had significantly fewer juveniles than families with two or more adults before the hunting season (single-adult broods, $\bar{x} = 2.76 \pm 0.28$, $n = 33$; >1-adult broods, $\bar{x} = 3.32 \pm 0.07$, $n = 492$, for broods with 1 and >1 adult; controlling for variation among years, $F = 6.61$, df = 5 and 519, $P = 0.01$).

Of yearlings associated with parents, 69% (47 of 68) were reobserved in subsequent years compared to 55% (17 of 31) of yearlings that did not associate with parents as yearlings. The difference, however, was not significant ($X^2 = 1.90$, df = 1, $P = 0.17$).

Sibling relationships.—Geese remained associated with brood mates throughout the first year of life by default due to the strong parent–offspring bonds. Sibling relationships (i.e. associated brood mates with or without parents) persisted past the first year, however, with 74%, 50%, and 39% of geese associating with brood mates as yearlings, two-year-olds, and three-year-olds and older, respectively (Table 6). As with parent–offspring bonds, there was a gradual decline over time in the proportion of siblings remaining with brood mates ($X^2 = 13.5$, df = 2, $P = 0.001$).

Sibling associations were not independent of parent–offspring relationships and, while the

TABLE 4. Percent (*n* in parentheses) of Greater White-fronted Goose offspring of different ages and sex associated with parents.[a]

Sex of offspring	Age of offspring			
	Juveniles[b]	Yearlings	Two-year-olds	Three-year-olds or older
Female	100 (102)	66.7 (48)	34.5 (29)	3.8 (13)
Male	100 (109)	70.6 (51)	44.0 (25)	25.0 (16)

[a] Offspring considered to be with parents if observed together at least once during year.

[b] By definition, all juveniles associated with parents.

TABLE 5. Percent of unmarked Greater White-fronted Geese in different social classes as determined from landing-group counts in Pacific Flyway, 1979–1982.

Season/ year	No. adults in group								No. juveniles			
		Adult groups			Adults with young					Groups[a]		With adults
	n	Single	Pair	>2	1	2	>2	Total	*n*	1	>1	
Autumn[b]												
1979–1980	456	5	25	39	1	22	7	30	185	2	0	98
1980–1981	1,899	5	24	40	1	18	12	31	867	2	2	95
1981–1982	1,390	7	29	30	1	23	10	33	775	3	4	93
Total	3,745	6	26	36	1	20	11	32	2,013	3	3	95
Winter[b]												
1979–1980	413	10	25	17	6	21	21	48	262	6	4	90
1980–1981	2,036	7	25	22	4	20	21	45	1,127	8	9	83
1981–1982	4,764	14	27	14	3	26	16	45	3,071	9	5	86
Total	7,213	12	27	16	3	24	18	45	4,515	9	6	85
Spring[d]												
1979–1980	375	3	22	20	3	26	26	55	228	4	7	89
1980–1981	765	7	30	13	4	25	22	50	519	8	11	81
1981–1982	520	13	28	20	3	22	16	40	252	9	4	87
Total	1,660	8	28	16	3	24	21	48	1,087	7	8	85

[a] Number of juveniles in group.

[b] Autumn was September to mid-October (before hunting season), winter was mid-October to mid-January (during hunting season), and spring was mid-January through early May (after hunting season).

latter could not always be distinguished (neck-banded siblings may have been associated with unmarked parents), the relative persistence of sibling bonds versus parent–offspring bonds after the first year was assessed by determining the proportion of time siblings spent with brood mates versus parents, when both were still known to be alive (Table 7). Yearlings and two-year-olds were more often associated with siblings (17% of both yearlings and two-year-olds were exclusively with siblings) than with parents (11% and 5% of yearlings and two-year-olds, respectively, were exclusively with parents). Differences between sibling affinities and sibling–parent affinities were only significant if yearling and two-year-olds were combined for analysis ($F = 4.28$, df = 1 and 112, $P = 0.04$). Neck-banded yearlings and two-year-olds spent more than 50% of the time alone (or with unmarked geese).

Multiple-adult associations.—Landing group counts revealed that multiple-adult groups ac-

TABLE 6. Prevalence of sibling associations in Greater White-fronted Geese wintering in southern Oregon and northern California, 1979–1989.[a]

Year of banding	Age of offspring							
	Juveniles[b]		Yearlings		Two-year-olds		Three-year-olds or older	
	No. geese	No. families	No. different geese	Percent with siblings	No. different geese	Percent with siblings	No. different geese	Percent with siblings
1979–1980	53	23	35	71.4 (11)[c]	21	52.4 (7)	7	28.6 (1)
1980–1981	76	26	39	64.1 (12)	11	18.2 (1)	2	100.0 (1)
1981–1982	88	23	36	86.1 (11)	18	66.7 (5)	9	33.3 (2)
Total	217	72	110	73.6 (34)	50	50.0 (13)	18	38.9 (4)

[a] Only includes observations of established groups with at least two neck-banded siblings known to be alive during year of observation.

[b] By definition, juveniles were in families and, hence, with siblings.

[c] Siblings considered to be together if observed together at least once during year. Number of different groups with two or more marked siblings known alive given in parentheses.

counted for nearly 50% of all wintering adult-plumaged geese, either as adult-plumaged groups, or mixed adult–juvenile groups (Table 5). The total number of adults in multiple-adult associations remained relatively constant throughout the year, but after hunting began the number of multiple-adult groups (groups without juveniles) decreased significantly ($X^2 = 382.75$, df = 1, $P < 0.001$), while the number of multiple-adult families (groups with juveniles) significantly increased ($X^2 = 16.65$, df = 1, $P < 0.001$).

Discussion

A large proportion of geese in this study was captured after the opening of the hunting season in mid-October, by which time many family groups were probably disrupted, as indicated by changes in the composition of landing groups (Table 5). Although monitoring changes in the status of members of partial families was sufficient for determining the persistence of family bonds, our inability to mark a representative sample of geese precluded using the marked sample to estimate the percent of the population in different social groups. Landing-group counts provided estimates of the proportion of juveniles and adult-plumaged geese in the population of different social classes, but did not allow differentiation among adult-plumaged geese.

Reunification of family members after banding.—The capability of goose families to reunite after banding has been reported for Greater White-fronted Geese (Miller and Dzubin 1965) and Canada Geese (*Branta canadensis*; Raveling 1969b). Raveling (1969b) used ratio telemetry to closely monitor regrouping in families of large Canada Geese, and found that most families had reunited within two days. My results are similar, given the high proportion (53%) of marked family members that were back together by the time members were first observed. Fidelity of geese to specific roost sites may facilitate reunification of social groups, as reported for Canada Geese (Raveling 1969b).

Influence of hunting.—Hunting contributed to the break-up of families by direct mortality of family members and by causing family members to become separated due to disturbance, as indicated by the reported kill rate and decrease in family unity after the beginning of the hunting season. Prevett and MacInnes (1980) found that Lesser Snow Goose (*Chen caerulescens caerulescens*) families were less stable in autumn than in winter, and attributed the difference (55 vs. 84% of families together each time they were observed) to disturbance and hunting at migration areas. In my study, family groups were less often intact during the hunting season, and geese also were more likely to be disturbed during this time (Ely 1992).

TABLE 7. Percent (±SE) of sightings for which yearling and two-year-old Greater White-fronted Geese were with siblings, parents, or alone.[a]

Status	Age of offspring	
	Yearlings ($n = 40$)	Two-year-olds ($n = 17$)
Alone[b]	55.2 ± 5.3	71.4 ± 6.3
With sibling(s)	17.0 ± 3.9	16.9 ± 6.8
With sibling(s) and parent(s)	16.6 ± 3.8	6.7 ± 2.9
With parent(s)	11.3 ± 2.7	5.0 ± 2.9

[a] Includes only neck-banded geese observed at least five different times in a given year when at least one neck-banded adult and two neck-banded offspring known to be alive at time of observation ($\bar{x}$ = 15.4 and 12.9 observations per individual for yearlings and two-year-olds, respectively).

[b] Geese not associated with other collared geese, but may have been with unmarked geese.

The propensity for geese captured before hunting to be in family groups also is an indication that family groups were fractured by hunting. However, disruption of families due to hunting may not have been the only reason why a greater proportion of birds captured before the hunting season were in families than at other times of the year (Table 1). Geese caught during September in the Klamath Basin were trapped at feeding sites (where families were more likely to be trapped), and also were likely from a different breeding area than geese caught at other times or locations (Ely and Raveling 1989, C. Ely and J. Takekawa in prep.). Also, peak numbers of Greater White-fronted Geese, Cackling Canada Geese (*B. c. minima*), Lesser Snow Geese, and Ross' Geese (*C. rossii*) usually did not arrive at staging and wintering areas in California and southern Oregon until after the opening of the hunting season, when the total number of geese often exceeded 500,000 (O'Neill 1979). Although Greater White-fronted Geese segregated from other goose species at roost sites, they commonly foraged in the same fields with other goose species (Ely 1992). The presence of large numbers of conspecifics, as well as other species of geese, undoubtedly made it

more difficult for separated geese to reunite with their family (Prevett and MacInnes 1980).

Parent–offspring relationships.—I may have underestimated the proportion of time family members were together in this study (76%; Table 3), as some neck-banded family members undoubtedly were not observed on occasions when family groups were in large milling flocks and/or tall vegetation. Raveling (1969b) reported that parents and juvenile Canada Geese were together 88 to 100% of the time, which is similar to values that Prevett and MacInnes (1980) reported for Lesser Snow Geese in the most settled situations (97%).

Owen (1980) summarized various studies and concluded that juveniles of *Anser* species generally remain with their parents throughout the first year of life, while in *Branta* break-up is more variable, and often occurs during the first winter. Findings in my study corroborate earlier work (but see Van Impe 1978) and reaffirm the strength of parent–juvenile bonds in geese, despite the destabilizing influences of hunting and disturbance.

Reports of yearling geese rejoining family groups have been largely anecdotal, and early researchers studying unmarked birds questioned whether multiple-adult groups represented extended family groups, temporary associations, "pseudo families," or bigamy (Boyd 1953, Lebret 1956, Lynch and Singleton 1964, Sherwood 1967). The occurrence of older offspring in goose families has been best documented by Raveling (1969b) and Prevett and MacInnes (1980), who reported that 15% of yearling Canada Geese (*B. c. interior*) and 10% of yearling Lesser Snow Geese, respectively, were associated with their parents. Two-year-old Lesser Snow Geese do not associate with their parents (Prevett and MacInnes 1980), although two-year-old Canada Geese occasionally rejoin their parents (D. G. Raveling pers. comm.). Although differing methodologies among studies make direct comparisons tenuous, it seems apparent that extended family bonds are more pronounced in Greater White-fronted Geese than in other species of goose studied to date. Similar observations have recently been reported by Warren et al. (1992) for Greenland White-fronted Geese (*Anser albifrons flavirostris*).

Geese (and swans) do not breed until they are two or, more commonly, three years of age (Owen 1980). Thus, substantial numbers of the adult-plumaged birds in the population are "prebreeders," whose social attachments are not predicated by caring for young. These birds have previously been reported to remain as singles, or form pairs (Owen 1980). The evidence I have presented suggests that many prebreeders do spend a good share of their time alone, but also remain associated with their parents and siblings until they are of breeding age, and beyond.

While I have demonstrated that many, if not most, multiple-adult groups probably are composed of family members from more than two generations, it is possible that some groups with more than two adult-plumaged geese represent other types of liaisons. Lorenz (1959) reported that both male–male and female–female relationships existed in Greylag Geese (*Anser anser*), although the latter were quite rare. Lamprecht and Buhrow (1987) reported polygynous groups to be fairly common in Bar-headed Geese (*A. indicus*), which they attributed at least in part to an excess of females in their semicaptive flock. Such "aberrant" nonfamily groups are probably rare in Greater White-fronted Geese, although the prevalence of long-term family bonds in this species makes it difficult to verify their existence, as it is difficult to determine if group members are related.

Sibling relationships.—Prolonged sibling associations in geese have rarely been reported (Owen 1980). Prevett and MacInnes (1980) found that 3% of two-year-old Lesser Snow Geese were still associated with brood mates, which is substantially less than found for Greater White-fronted Geese during my study (18–67%, $\bar{x}$ = 50%). If Prevett and MacInnes had controlled for mortality and neck-band loss (analyses not limited to sightings when brood mates known to be alive), the proportion of older geese calculated to be with siblings (and parents) may have been higher. The large proportion of Greater White-fronted Geese that maintained sibling bonds after their second winter (40–50%; Table 6) and the greater affinity of older offspring for brood mates than parents are unprecedented in waterfowl, and suggest that long-term sibling bonds may be very important in many aspects of the behavioral ecology of geese.

Implications of parental care.—Extended parent–offspring relationships within waterfowl (Anatidae) have been best documented in swans (genus *Cygnus*; Evans 1979, Scott 1980a, b, 1984,

1988, Braithwaite 1981, Mathiasson 1987). Scott (1980b) found that two- and three-year-old Bewick's Swans (*Cygnus columbianus*) were most dominant when they were associated with their parents, and partially attributed this latent parental dependence in swans to physical immaturity of even three- and four-year-old subadults. However, Scott (1980b) also reported that Bewick's Swan parents actively repulsed older offspring, a behavior which was observed very infrequently in my study. Young Greater White-fronted Geese are nearly as large in size and mass as adults in their second winter (unpubl. data); parents may be more tolerant of their older offspring than parental swans as juvenile geese may be less dependent on parental protection than juvenile swans, and there may be less intraspecific competition for food.

Large families of Greater White-fronted Geese are dominant over smaller families, pairs without goslings, and single individuals (Boyd 1953). Although the dominance rank of extended family groups in my study was not known, it seems likely that families containing older offspring may have had the highest dominance rank as they would usually have had more members than families without more than one generation of offspring. Dominant social groups may have increased access to limited food and safe roost sites (Raveling 1966, 1970, Black and Owen 1989b), both of which are potentially limiting to Greater White-fronted Geese wintering in California and southern Oregon, as evidenced by significant declines in body mass during winter (Ely and Raveling 1989), and high mortality from hunting (Timm and Dau 1979).

I could not demonstrate that yearlings associating with parents accrued any survival benefit. Results are somewhat equivocal, however, as sample sizes were small and do not reflect the proportion of associated and nonassociated yearlings that survived to breeding age. In some instances, family behavior may be a liability, particularly in populations in which hunting is a major cause of mortality (Hanson and Smith 1950). Prevett and MacInnes (1980) suggested that Lesser Snow Geese with no social bonds may be the least vulnerable to hunting because the searching behavior of separated family members makes them easier to decoy and shoot.

Older offspring in my study maintained a greater distance from parents than juveniles; it seems unlikely that parents incurred additional costs by allowing older offspring to remain with families in terms of an increased vigilance (Lazarus and Inglis 1986) or competition for limited food. Indeed, Barnacle Goose (*Branta leucopsis*) parents that keep juveniles the longest have been shown to be more successful in rearing young the following year (Black and Owen 1989a). Benefits to parents are also evident on the breeding grounds where yearling and occasionally older offspring (nonparental adult-plumaged geese) remain near their parents' nest until late in incubation, and actively protect the nest from predators (Ely 1979, in prep.).

The smaller brood sizes of Greater White-fronted Goose families that were attended by just one adult may indicate that single-adult families are less successful than families with at least two adults. This is in contrast to the findings of Martin et al. (1985) who questioned "the extent to which parental care requirements constrain mating systems, particularly for precocial species," despite finding that in one of two years of study, biparental families of Lesser Snow Geese were more successful in fledging young than uniparental families. Although geese are precocial in early physical development, social processes develop slowly, and it is likely that extended parental care in Greater White-fronted Geese enhances social development.

Extended parental care in Greater White-fronted geese increases the likelihood of parent–offspring conflict (Trivers 1974). Although young Greater White-fronted Geese appear to extend the period of potential conflict, the conflict may not be as acute as in other avian species. Benefits probably outweigh costs, at least until the extended family becomes too large to function as a social unit and/or subadults become too numerous and compete with their parents and younger siblings.

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