

Buffered Development: Resilience after Aggressive Subordination in Infancy

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ABSTRACT: Do aggressive dominance and subordination in vertebrate broods and litters affect development? We examined 1,167 fledglings from two-chick broods of the blue-footed booby (*Sula nebouxi*), a species in which the first-hatched chick dominates with violent attacks throughout the nestling period and subordinates suffer lower fledging success, but if both broodmates survive, they grow to the same size. There was little evidence that dominant fledglings were more likely to recruit into the breeding population than were subordinate fledglings, and there was no evidence that dominant and subordinate recruits differed in their age, date, brood size, or nest success at first reproduction or in their summed brood sizes or total nest success over the first 5 yr or first 10 yr of life. Compared with dominants, subordinate fledglings were less prejudiced by late hatching and established clutches earlier over the first 10 yr, and subordinate recruits had 33% larger broods over the first 5 yr. However, in broods where both chicks fledged, accumulated reproductive success for chicks up to age 5 yr was similar for dominants and subordinates. Exercising dominance throughout infancy apparently does not fortify a chick for the future and may incur a long-term cost, and suffering violent subordination throughout infancy has little or no prejudicial effect and may even steel a chick for adult life.

Keywords: dominance, siblings, infants, broods, development, booby.

Ethologists and developmental psychologists have asserted the fundamental importance of experience and particularly social interactions during infancy in the behavioral de-

velopment of humans and other vertebrates (e.g., Freud [1905] 1938; Hebb 1949; Hess 1959; Harlow and Harlow 1962; Rosensweig and Bennett 1969). In humans, interactions of infants with parents have traditionally been viewed as primordial, but the substantial (yet neglected) influence of interactions with peers is now recognized (Harris 1998). In many species of birds and mammals, the main social milieu in which the infant develops is the sibling group, which opens the door to long-term effects of broodmates and littermates on development. Some influences are undoubtedly benign, but sibling competition could have prejudicial effects, and individuals might even manipulate the developmental flexibility of future rivals for long-term selfish benefit (Geist 1978; Huntingford and Turner 1987). Surprisingly, although some laboratory studies have looked for developmental effects of postpartum litter composition on behavior after the period of cohabitation with littermates (e.g., Mendl and Paul 1990), to our knowledge, there has been no field study of long-term effects of social interaction with siblings in any vertebrate species.

Aggressive dominance hierarchies among infants potentially have long-term effects because they typically involve consistent interactions with punishing or reinforcing stimulation and high levels of arousal and because dominance status potentially persists beyond infancy. In birds, dominance hierarchies among broodmates have been reported for raptors, herons, pelicans, boobies, cormorants, anhingas, ibises, skuas, gulls, guillemots, oystercatchers, cranes, grebes, and kingfishers as well as several species of gallinaceous birds and waterfowl with fully precocial chicks (reviews in Mock and Parker 1997; Drummond 2001a, 2002). In mammals, aggressive littermate hierarchies are reported for canids (Fox and Clark 1971; Bekoff 1978, 1981b, 1989), rabbits (Whitworth and Southwick 1984), pigs (McBride 1963; Fraser 1975), hyenas (Frank et al. 1991; Smale et al. 1995, 1999), and rodents (Taylor 1980; Meaney and Stewart 1981; Takahashi and Lore 1983). In adult vertebrates in general, high dominance rank is often associated with greater copulatory success, higher reproductive success, preferential access to resources, increased

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survival of progeny, and diverse physiological and behavioral effects (Dewsbury 1982). Despite frequent suggestions and some indirect evidence that dominance hierarchies in broods and litters might affect competitive abilities, status, or reproductive success in later life (e.g., Geist 1978; Bekoff 1981a; Simmons 1988; Spear and Nur 1994; Frank 1996; Thomas et al. 1999), no data have yet provided a credible test for any species.

We looked for long-term effects of agonism between infant siblings in the blue-footed booby (*Sula nebouxii*), whose characteristic two-chick brood shows an extreme, archetypical relationship of dominance-subordination (Nelson 1978; Drummond et al. 1986) coupled with differential mortality of the subordinate nestling. Always one broodmate dominates by threatening and delivering powerful pecks to the other's cranium, nape, and body every day, while the other (after some initial resistance) largely assumes a subordinate role by cowering, adopting stereotyped submissive postures, and declining to attack. The relationship usually persists from shortly after hatching until independence more than 4 mo later (Drummond et al. 1991), provided food shortage does not induce the dominant chick to intensify attacks and kill its sibling (Drummond and García Chavelas 1989; Drummond 2001b). Experiments have shown that both are learned roles (trained winner and trained loser) that persist for many days even when the broodmate is replaced by a different individual (Drummond and Osorno 1992; Drummond and Canales 1998). Also, during the first few weeks, subordinate nestlings typically show double the normal level of circulating corticosterone (Nuñez de la Mora et al. 1996), a hormone that is associated with submissiveness (Leshner 1980, 1981, 1983) and tends to produce long-term pathologies when high levels are maintained over days or weeks (Sapolsky 1992). Moreover, when subordinate nestlings are induced to overthrow aggressively a much smaller experimental broodmate raised in a dominant role, they usually fail, which implies an acquired physiological or psychological weakness (Drummond and Osorno 1992) with possible long-term effects.

Unless development of boobies is buffered against repeated violent impacts, consistent psychological subordination, and elevated corticosterone (with potential organizational effects) during the 4 mo of infancy, growing up as a subordinate could in principle prejudice perceptual and motor abilities, learning ability, foraging skills, social competitive skills, or attractiveness. Persistent deficits in any of these domains should be reflected by diminished recruitment into the breeding population or depressed reproductive success. Therefore, to test for long-term behavioral deficits as a result of subordination during infancy or long-term behavioral strengths as a result of exercising dominance during infancy, we screened for differences in

the recruitment and adult reproductive performance of subordinate and dominant chicks.

The particular biology of blue-footed boobies allows us to discount two potential confounds of longitudinal descriptive studies on this topic. First, preexisting individual differences can determine status in a sibship hierarchy and become confounded with effects of the hierarchy. For example, firstborn piglets are larger, obtain preferred teats, outfight littermates for access, consume more milk, and grow faster (Hartsock and Graves 1976), and effects of agonistic experience per se are confounded with cascading effects of genetic inheritance and prenatal environment (e.g., Hayssen 1984; vom Saal 1989). Agonistic rank in blue-footed booby broods is not usually associated with innate competitive prowess or individual differences but assigned by hatching order, and hatching order is not related to egg size (Drummond et al. 1986) or to egg hormone content (H. Schwabl et al., unpublished data). Second, infant dominance hierarchies often engender variation in growth attainment such that differential performance after the end of parental care could be attributed either to agonistic experience during infancy or to size at independence. For example, little egrets (*Egretta garzetta*) of high pre fledging size rank (but unknown hatch order) within the brood showed high breeding success in later seasons (Thomas et al. 1999), but we cannot tell whether agonistic experience or fledging size (or some other factor such as congenital vigor) was responsible. Blue-footed booby subordinates and dominants are similar in linear dimensions and mass at the time they fledge (Drummond et al. 1991; this study).

Methods

General

At the breeding colony of the blue-footed booby on Isla Isabel, Nayarit, Mexico (21°52'N, 105°54'W), between 1989 and 1995, we recorded the postfledging survival and reproduction of all senior and junior (first- and second-hatched) chicks that fledged from two-chick broods in our two study areas that measured 20,800 m² and 6,089 m² and lay roughly 400 m apart. We excluded the cohorts of 1990, when no fledglings were banded, and 1992, when no chicks fledged because of El Niño, and deleted any broods used in experiments. A sample of 1,167 fledglings was obtained from five cohorts (of seniors and juniors, respectively): 1989 (170 and 141), 1991 (113 and 98), 1993 (106 and 82), 1994 (189 and 169), and 1995 (52 and 47). In every cohort, there were fewer juniors than seniors because juniors suffer differential mortality in the nestling period (Nelson 1978; Drummond et al. 1991; Torres and

Drummond 1997). Reproductive histories of all cohorts were followed through 1999.

In every breeding season from 1989 to 1999, from shortly after the start of hatching, we marked all nests in the study areas with a clutch or brood with numbered wooden stakes and censused them and any new nests over a period of roughly 5 mo until the end of the fledging period. We also included any nest within 20 m of the borders of the study areas if one of the adults was banded. Importantly, banded birds were rarely detected outside this 20-m margin. Laying, hatching, and survival of eggs and chicks were recorded every 3 d until most chicks had reached age 30 d and thereafter every 6 d until age 70 d (at this age, males and females have reached roughly 100% and 98% of their asymptotic beak and ulna lengths, respectively, and completed 76% of the time needed to become fully feathered). Within 3 d of hatching, chicks were marked with colored leg bands, which were replaced by numbered plastic bands at age 7–10 d and then by numbered steel bands at age 70 d. The breeding session in 1989 was exceptional in that chick survival was recorded every 3 d until chicks became fully feathered (males at $\bar{X} = 86$ d, females at $\bar{X} = 92$ d; Drummond et al. 1991). Chicks were considered fledglings, and each one was measured (beak and ulna, ± 1 mm) when it was 70 d old (cohorts 1991–1995) or when it became fully feathered (cohort 1989). Importantly, size-based sex identification (Drummond et al. 1991; Torres and Drummond 1997) was possible only for the 1989 cohort. Nestlings that hatched before the start of censuses were measured at the first census to estimate their age using growth curves for beak and ulna.

Our sampling and inferences partly depend on the untested assumption that senior and junior chicks do not differ systematically in natal dispersal or breeding dispersal and therefore could be sampled equitably. Available data suggest that the boobies of Isla Isabel are highly philopatric and faithful over at least several years to the neighborhood where they were born. Nearly 40% of banded fledglings in this study returned to breed in our two study areas on Isla Isabel. When studying two of the closest colonies of blue-footed boobies on the Islas Marietas and Isla San Pedro Mártir, which are 130 and 903 km distant, we have not detected any boobies banded as fledglings or adults on Isla Isabel. Male recruits to the Isla Isabel colony nested 2–111 m (median = 24.1 m) from their natal nest sites, female recruits nested 4–150 m (median = 28.3 m) from their natal sites, and neither sex strayed further from the natal nest on its subsequent nesting attempt (Osorio-Beristain and Drummond 1993). If intraspecific competition drives natal dispersal (Murray 1967; Waser 1985), then less dominant or competitive individuals should disperse farther from the natal site (Tonkyn and Plissner

1991). This relationship has been observed in numerous species (Gauthreaux 1978) including the black kite (*Milvus migrans*), in which second-hatched male fledglings dispersed farther than did first-hatched males (Forero et al. 2002). If subordinate blue-footed boobies disperse farther than do dominants, the bias thereby introduced into our sampling of survival and recruitment would be conservative and would tend to mask the equal or superior performance by juniors that we report in “Results.” However, if among subordinates dispersal varies inversely with competitiveness, a liberal bias could be introduced into our sampling of the reproductive performance of recruits. Of course, the inevitable dispersal of some individuals away from our study areas should result in us underestimating to an unknown degree the recruitment and accumulated reproductive success of both senior and junior fledglings.

We assumed that the senior member of each brood was dominant throughout cohabitation of the two chicks since dominance inversions are uncommon (e.g., Drummond et al. [1991] recorded only one dominance inversion in 27 broods observed every 4 d from hatching through fledging of both broodmates). We compared senior and junior fledglings for recruitment (proportion that subsequently established a nest in any year); age at first nesting; and laying date, brood size, and nest success (number of fledglings produced) at first nesting, during the first 5 yr of life, and during the first 10 yr of life. The independent variables of most interest were seniority and duration of cohabitation. The death of either a senior or a junior nestling curtails its broodmate’s period of exposure to sibling treatment (dominance or subordination) to as little as a single day of cohabitation, and longer periods of cohabitation should have a greater effect on development.

Data Analysis

In many analyses, we included cohort and hatching date of fledglings among the independent variables not because these factors are central to our question but to control the variance as a result of factors that commonly influence the reproduction of birds.

Recruitment. Recruitment was analyzed using a generalized linear model with binomial distribution of errors and a logit link function (Crawley 1993). Each fledgling from the five cohorts (1989–1995) was classified as a recruit if it nested in any year up to 1999 and as a nonrecruit if it did not. The model included seniority and cohort as factors and hatching date and the duration of the sibling cohabitation as continuous variables. Because we were more interested in detecting effects of hatching date on recruitment than we were in comparing magnitudes of effect among years, post hoc comparisons compared the

slope of each cohort with 0 rather than comparing cohorts with each other. In an additional analysis, we included only pairs of broodmates in which both of them fledged; in this sample, all subjects were effectively exposed to sibling interaction throughout infancy, which gave maximal scope for sibling developmental influence to be expressed.

In addition, the recruitment of fledglings from the 1989 cohort was analyzed separately with a model that included the sex of fledglings. This allowed us not only to determine separately for males and females whether they were affected by seniority but also to look for effects of body size at fledging on recruitment while controlling for the large size difference between males and females.

Reproduction. We used generalized linear models with normal error distribution and an identity link function (Crawley 1993) to analyze age at first reproduction and reproductive performance (laying date, brood size, and nest success) at first nesting, during the first 5 yr after fledging, and during the first 10 yr after fledging (only recruits from cohort 1989). Later cohorts had fewer years in which to recruit, so we homogenized the variance among cohorts in age of first nesting by dividing each bird's age of first nesting by the total number of years available to its cohort for nesting. Consequently, no importance was attached to significant differences between cohorts in age of first nesting. The analysis of age at first nesting included cohort, seniority, and sex as categorical factors. To compare treatment means (cohorts/seniority/sex), a priori planned comparisons were performed. Cohort 1995 was not included in this analysis because it had only 4 yr in which to nest, an insufficient period to evaluate age at first reproduction.

To control for variation among years, the laying date, brood size, and nest success (number of fledglings) of each bird's first nest were centered by subtracting the mean value of the colony in the same year (McCleery and Perrins 1988). The analyses of these variables included cohort, seniority, and sex as categorical factors. Centered laying date was log transformed because the residuals were overdispersed.

To analyze reproductive performance during the 5 yr after fledging, all response variables in each reproductive attempt were centered as previously described. We analyzed the mean centered laying date of all attempts in the period, the summed centered brood sizes for all attempts, and the total centered numbers of fledglings produced in all attempts. To analyze the reproductive performance of recruits from cohort 1989 during the first 10 yr after fledging, we used the mean centered laying dates and the summed absolute values of brood size and fledglings produced in all reproductive attempts. Brood size and number of fledglings were not centered in this last analysis because

data were from the same cohort of recruits observed over the same period of time.

Birds that made more than one breeding attempt in the same year (36 out of 434 birds in the first-nest analyses, 62 out of 397 birds in the 5-yr analyses, and 78 out of 183 birds in the 10-yr analyses) were included only once for the year. In the first-nest and 5-yr analyses, we used the bird's earlier date, larger brood size, and larger nest success for the season. In only four cases in the first-nest analyses and seven cases in the 5-yr analyses did data for laying date, brood size, and nest success come from different breeding attempts. In the 10-yr analyses, where brood sizes and numbers of fledglings were not centered, we used the bird's earlier date in each year and the summed absolute brood sizes and summed fledglings produced in both reproductive attempts in the same season.

Comparisons of Broodmate Pairs. In an additional suite of analyses, we compared the reproductive performance of each junior recruit with that of its own broodmate using all broods where both birds not only fledged but also were recruited into the breeding population (and taking their sex into account). Furthermore, we compared the absolute total nest success of each pair of fledgling broodmates over the first 5 yr of life using all broods where both birds fledged, whether zero, one, or two chicks recruited (here, sex could not be taken into account). This last analysis combined the information of recruitment and reproduction to yield a comparison of the accumulated reproductive success of seniors and juniors up to age 5 yr. Such samples are necessarily smaller and somewhat less representative than are our complete samples, but they are particularly apt for detecting systematic differences between siblings (Berbaum and Moreland 1980; Sutton-Smith 1982), and they give excellent and unique control over potentially important sources of variation such as cohort, hatching date, quality of parents, genetic quality of fledglings, and nest site. We used two-factor ANOVAs (seniority \times brood sexual composition) with split-plot design (Kirk 1968) and matched subjects (senior and junior broodmates). Significant interactions were explored with tests of simple main effects (*t*-tests), and values of Type I error were adjusted using the Dunn-Šidák method (Sokal and Rolf 1995).

Size at Fledging. We examined size of each sex at fledging to discount size as a possible explanation for differential performance of seniors and juniors. The samples for these analyses were all recruits of cohorts 1991–1995 (for which sex was known only for recruits) and all fledglings of cohort 1989. Cohorts 1991–1995 and cohort 1989 were analyzed separately because they were measured at different ages. For both samples, we used generalized linear models

with normal error distributions and an identity link function (Crawley 1993) to compare the natural logarithms of beak and ulna lengths of seniors and juniors at fledging and also to seek associations between their size at fledging and their brood size and nest success at first reproductive attempt (both variables centered), while controlling for cohort, hatch date, and length of cohabitation.

Power Analyses. To help interpret statistical tests where seniority was not significant as a main effect or in any interaction, at the end of "Results," we provide measures of sensitivity that are based on an α level of 0.05 and power of 0.80. For logistic regressions, we calculated the minimum correlation coefficient detectable using NCSS, 2001; for generalized linear models and ANOVA, we calculated the sample size that would be required to detect a significant difference using JMP, 1989–1997, by SAS.

Results

Sample values are expressed throughout as $\bar{X} \pm SE$. Small inconsistencies in sample sizes are due to exclusion of individuals whose laying date was not known, whose sex could not be confirmed, or who eluded banding.

Recruitment

Taking together senior and junior fledglings (of both sexes), we found that the probability of recruitment varied among cohorts (main effect cohort; table 1). The proportion of fledglings recruited from each cohort was 0.59, 0.27, 0.21, 0.40, and 0.30 for 1989, 1991, 1993, 1994, and 1995, respectively, and yielded an average of 0.35 for the five cohorts. Overall, there was no difference in the recruitment of senior (41%) and junior (37%) fledglings (main effect seniority; table 1). However, when each cohort was analyzed separately (interaction term cohort \times seniority; table 1), senior fledglings of 1991 and 1993 were more likely to be recruited than were junior fledglings (1991 cohort: $P = .001$; 1993 cohort: $P = .05$; fig. 1A). There was no significant difference in cohorts 1994 and 1995, and junior fledglings from cohort 1989 had a marginally greater probability of recruitment ($P = .06$) than did senior fledglings (fig. 1A).

Hatch date was a good predictor of the probability that a fledgling would return to the colony as a breeding adult, and the effect of hatch date was similar for seniors and juniors (table 1). Overall, the probability of recruitment decreased with hatching date, and the rate of decrease varied among cohorts (main term and interaction; table 1; fig. 1B). Recruitment probabilities decreased substantially with natal date in some cohorts but not in others. Probability of recruitment declined with hatching date by

Table 1: Recruitment of senior and junior fledglings from broods of two in cohorts 1989–1995

Variable	χ^2	df	<i>P</i>
Maximal model:			
Hatch date	29.52	1	<.0001
Cohort	17.62	4	.001
Seniority	.04	1	.83
Cohabitation	13.93	1	.0001
Hatch date \times cohort	18.53	4	.0009
Hatch date \times seniority	1.27	1	.25
Hatch date \times cohabitation	.11	1	.74
Cohort \times seniority	20.47	4	.0004
Cohort \times cohabitation	3.15	4	.53
Seniority \times cohabitation	3.29	1	.06
Minimal adequate model:			
Hatch date	35.31	1	<.0001
Cohort	17.90	4	.001
Seniority	1.48	1	.22
Cohabitation	15.61	1	<.0001
Hatch date \times cohort	18.32	4	.001
Cohort \times seniority	18.36	4	.001

Note: $N = 1,167$. To obtain the minimal adequate model, backward model simplification was performed. None of the third and fourth degree interactions were significant, so they are not reported.

37% in cohort 1989 ($t = 2.22$, $P = .02$), 54% in cohort 1991 ($t = 3.89$, $P = .0001$), and 63% in cohort 1994 ($t = 3.48$, $P = .0005$), but the slopes of the adjusted curves were not significantly different from 0 in cohorts 1993 ($t = 1.41$, $P = .15$) and 1995 ($t = .15$, $P = .88$; $df = 1,151$ in all t -tests; fig. 1B; percentages calculated from extremes of adjusted curves).

The longer a fledgling had cohabited with its sibling, the less likely it was to be recruited (main term; table 1), and seniors and juniors did not differ significantly in this respect even when variation as a result of cohorts and hatch date was considered (interaction terms; table 1; fig. 1C). Pooling data from all cohorts, we found that on average, the probability of recruitment of senior and junior fledglings whose younger broodmate died a day after the start of cohabitation was approximately 18% greater than that of fledglings whose broodmate survived up to fledging (fig. 1C).

Results were similar when we analyzed only those 927 fledglings whose sibling was present throughout infancy. Recruitment was similar for seniors (42%) and juniors (36%) and declined significantly with hatchdate (by as much as 97% in cohort 1991; $t = 2.07$, $P = .03$), and seniors of cohorts 1991 and 1993 significantly outperformed juniors. Contrary to expectation, decline in recruitment with natal date was greater for senior (44%) than for junior (9%) fledglings (hatch date \times seniority: $\chi^2 = 4.49$, $df = 1$, $P = .03$), and cohorts did not differ

significantly in this respect (hatch date \times seniority \times cohort: $\chi^2 = 3.04$, $df = 4$, $P = .55$).

In cohort 1989, there was a similar pattern, with similar proportions of senior (55%) and junior fledglings (64%) recruited and a decline in recruitment with hatch date, which may have been steeper for seniors than for juniors (hatch date \times seniority: $\chi^2 = 3.43$, $df = 1$, $P = .06$). Neither beak length nor ulna length at the time these birds became fully feathered explained a significant proportion of variance in the probability of recruitment (beak length \times sex: $\chi^2 = 2.82$, $df = 3$, $P = .42$; ulna length \times sex: $\chi^2 = 5.51$, $df = 3$, $P = .13$).

Reproduction

Age at First Nesting. Overall, senior and junior recruits did not differ in their age at first reproduction ($F = 0.87$, $df = 1, 401$, $P = .35$; fig. 2). Most of the variation in the analysis was related to sex ($F = 16.34$, $df = 1, 401$, $P < .0001$) and to the year a bird hatched (cohort: $F = 26.50$, $df = 3, 403$, $P < .0001$), although this last effect may not be genuine because sampling of different cohorts was inequitable (see "Data Analysis"). The difference in the age of males and females at first reproduction was similar for all cohorts and for both seniors and juniors (sex \times cohort: $F = 0.78$, $df = 3, 396$, $P = .50$; sex \times seniority: $F = 0.40$, $df = 1, 394$, $P = .52$). The interaction terms seniority \times cohort ($F = 3.64$, $df = 3, 396$, $P = .01$) and seniority \times cohort \times sex ($F = 3.46$, $df = 3, 393$, $P = .01$) were significant. However, when we used post hoc comparisons to explore the interactions for effects of seniority, only junior male recruits from cohort 1991 differed significantly from any other seniority/sex/cohort group (18 senior vs. nine junior males, 1991: $t = 4.61$, $df = 390$, $P < .0001$; $P > .5$ in the other seven pairwise comparisons). Furthermore, when cohort 1991 was excluded from the analysis, none of the interaction terms was significant, and variation by cohort and sex, but not by seniority, explained a large and significant proportion of the variation in age at first reproduction (cohort: $F = 41.22$, $df = 2, 342$, $P < .0001$; sex: $F = 12.74$, $df = 1, 346$, $P = .0004$; seniority: $F = 0.05$, $df = 1, 346$, $P = .82$). Hence, any effect of seniority on age of reproduction was negligible.

Pooling all cohorts, we found that the majority of male (93%) and female (92%) recruits bred for the first time during the first 5 yr of life, with females starting nearly half a year earlier than did males (3.85 ± 0.08 vs. 4.32 ± 0.09 yr; $N = 179$ females, 227 males; fig. 2).

Date of First Nest. There was no difference between senior and junior recruits in the laying date of their first reproduction (seniority: $F = 1.45$, $df = 1, 352$, $P = .22$), even

when possible variation associated with cohort (cohort \times seniority: $F = 0.10$, $df = 4, 346$, $P = .98$) and sex (sex \times seniority: $F = 0.001$, $df = 1, 343$, $P = .97$; seniority \times cohort \times sex: $F = 0.49$, $df = 1, 342$, $P = .77$) was considered. Overall, females established their first

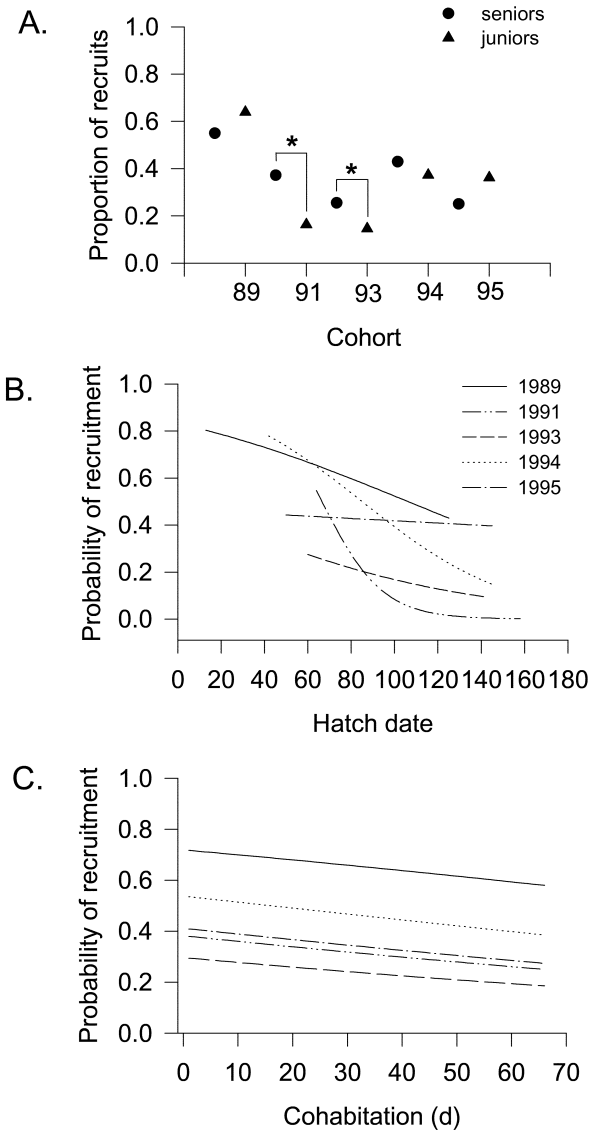


Figure 1: Recruitment of senior versus junior fledglings from cohorts 1989–1995. Analyzed according to (A) cohort (post hoc comparisons; asterisk indicates $P \leq .05$), (B) hatch date, and (C) duration of cohabitation with the broodmate, using a generalized linear model with binomial error distribution. The model included cohort and seniority as factors and hatch date and duration of sibling cohabitation as continuous variables. The parameters of the adjusted curves were estimated from the minimal model ($r = 0.12$, $df = 1, 152$, $P < .0001$; table 1). Hatch date 1 = January 1. Number of senior/junior fledglings: 1989, 170/141; 1991, 113/98; 1993, 106/82; 1994, 189/169; 1995, 52/47.

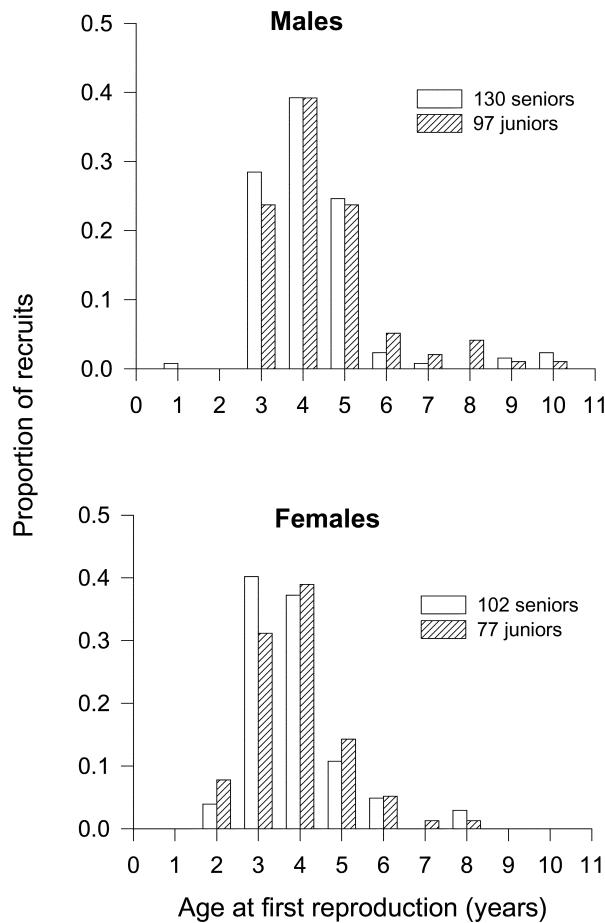


Figure 2: Age at first reproduction of senior and junior recruits from cohorts 1989–1994. Number of recruits: cohort 1989, 183; 1991, 56; 1993, 32; 1994, 135.

clutch an average 10 d earlier in the season than did males (mean departures from the colony’s average laying date in each year were -3.08 ± 29.27 d for 157 females and 7.28 ± 38.52 d for 201 males; $F = 5.46$, $df = 1, 352$, $P = .02$), and although cohorts differed in (centered) laying date (cohort: $F = 2.69$, $df = 4, 355$, $P = .03$), the difference between the sexes was similar in all cohorts (cohort \times sex: $F = 0.92$, $df = 4, 346$, $P = .45$).

Brood Size and Nest Success at First Nest. At first reproductive attempt, senior and junior recruits did not differ in brood size or nest success (both variables centered), even when variation by sex and cohort was considered (table 2). Male and female first breeders did not differ either. There were differences among cohorts in brood size but not in nest success (table 2). Except for the 1989 cohort, brood sizes of all cohorts were negative (below the colony mean; cohort 1989: 0.08 ± 0.05 chicks; cohort

1991: -0.05 ± 0.11 ; cohort 1993: -0.18 ± 0.15 ; cohort 1994: -0.25 ± 0.07 ; cohort 1995: -0.29 ± 0.15 ; colony mean for the period 1991–1999: 0.92 ± 0.009). Not surprisingly, nest success was negative for all cohorts (first breeders: -0.13 ± 0.03 fledglings; colony mean nest success for the period 1991–1999: 0.65 ± 0.008 fledglings).

Reproduction during First 5 Yr. Senior and junior recruits did not differ in any of the three (centered) measures of reproductive performance over the first 5 yr of life, even when cohort and sex were taken into account (table 3). Mean laying date varied among cohorts, and overall, females established a clutch approximately 10 d earlier than did males (-3.40 ± 2.25 d, $N = 190$ males; -12.69 ± 1.81 d, $N = 166$ females). However, seniors and juniors were similar in laying date, summed brood sizes (summed over the 5 yr), and total nest success (number of fledglings produced over the 5 yr).

Reproduction during First 10 Yr. Senior and junior recruits of the 1989 cohort differed on only one measure of reproductive performance over the first 10 yr of life: laying date (table 4). Sex was included in the model but did not affect any of the measures. On average, the 88 junior recruits established their clutches roughly 7 d earlier than did the 90 senior recruits and 11 d earlier than the colony average (juniors: -11.22 ± 1.68 d; seniors: -4.69 ± 2.27 d; table 4).

In our samples, juniors of both sexes tended to outperform seniors in absolute summed brood sizes and absolute total nest success over the 10 yr, but none of the differences was significant (table 4). Summing over 10 yr, we found that the absolute summed brood sizes of senior and junior male recruits, respectively, were 4.21 ± 0.43 versus 4.76 ± 0.43 hatchlings and that those of senior and junior female recruits, respectively, were 4.43 ± 0.47 versus 4.90 ± 0.48 hatchlings. The mean absolute total nest

Table 2: Brood size and nest success at first nest of senior and junior recruits from broods of two in cohorts 1989–1995

Variable	df	Brood size		Nest success	
		F	P	F	P
Cohort	4	3.63	.006	2.02	.09
Seniority	1	.36	.54	.12	.72
Sex	1	1.44	.23	2.99	.08
Cohort \times seniority	4	1.14	.33	.81	.51
Cohort \times sex	4	.93	.44	.98	.41
Seniority \times sex	1	.85	.49	.12	.72
Cohort \times seniority \times sex	4	.71	.58	1.06	.37

Note: Centered brood size and nest success were analyzed. Number of recruits: cohort 1989, 183; 1991, 56; 1993, 32; 1994, 135; 1995, 28.

Table 3: Mean laying date, summed brood sizes, and total nest success during the first 5 yr after fledging of senior and junior recruits from broods of two in cohorts 1989–1995

Variable	df	Laying date		Brood size		Nest success	
		F	P	F	P	F	P
Cohort	4	4.52	.001	1.68	.15	.79	.53
Seniority	1	.22	.63	1.50	.22	1.09	.29
Sex	1	9.48	.002	3.55	.06	1.42	.23
Cohort × seniority	4	.24	.91	1.22	.30	1.16	.32
Cohort × sex	4	1.34	.25	.51	.72	.29	.88
Seniority × sex	1	.58	.44	2.97	.08	.16	.68
Cohort × seniority × sex	4	.50	.73	.50	.73	1.16	.32

Note: All variables were centered. Number of recruits for the analyses of brood size and nest success: cohort 1989, 159; 1991, 47; 1993, 29; 1994, 134; 1995, 28. Forty-one recruits were excluded from the analysis of laying date because their dates were unknown.

success of senior and junior males, respectively, was 3.05 ± 0.37 versus 3.35 ± 0.35 fledglings, and that of senior and junior females, respectively, was 2.87 ± 0.36 versus 3.53 ± 0.39 fledglings ($N = 54$ senior males, 51 junior males, 38 senior females, and 40 junior females).

Comparisons of Broodmate Pairs

In the 81 pairs of fledglings (from five cohorts) where both birds recruited, juniors tended to perform slightly better than did seniors. Junior recruits in broods of all four sexual compositions tended to hatch and possibly fledge more offspring than did their own senior siblings over the first 5 yr of life. Over that period, juniors’ summed absolute brood sizes were 33% greater than those of their senior siblings, and their total nest success exceeded that of their senior siblings by 39%, although the latter effect fell short of significance ($P = .06$; table 5). In the analyses of brood size and nest success at first reproduction and over the first 10 yr of life, junior recruits also tended to outperform their elder siblings but not significantly (table 5). Junior recruits differed from their own broodmates in laying date, but the effect varied with the sexual composition of the brood (table 6). At first reproduction and during the first 5 yr of life, junior recruits from male-male broods nested earlier than did their siblings (first nest: $t = 2.33$, $df = 17$, $P = .03$; first 5 yr: $t = 2.86$, $df = 15$, $P = .01$), while junior recruits from female-male broods (female with younger brother) nested later than did their siblings (first nest: $t = 2.85$, $df = 15$, $P = .01$; first 5 yr: $t = 2.52$, $df = 13$, $P = .02$).

In the 460 pairs of broodmates (from five cohorts) where both fledged but did not necessarily recruit, accumulated reproductive success up to age 5 yr was similar for seniors and juniors. Absolute total nest success up to

age 5 yr was 0.448 versus 0.415 fledglings, for seniors and juniors, respectively (seniority: $F = 0.33$, $df = 1, 455$, $P = .57$; cohort: $F = 8.76$, $df = 4, 455$, $P < .001$; seniority × cohort: $F = 1.89$, $df = 4, 455$, $P = .11$). This result integrates recruitment and reproductive performance.

Size at Fledging

Seniors and juniors of both sexes did not differ significantly in size at fledging either in the samples of 70-d-old recruits from cohorts 1991–1995 or in the sample of all fully feathered fledglings in the 1989 cohort. Notably, among 20 contrasts of size, in only eight cases did the mean value for seniors exceed that of juniors, and duration of cohabitation had no effect on size of seniors or juniors of either sex. Furthermore, in neither of these samples of cohorts was size at fledging of either sex significantly related to performance at first reproduction.

Power Analyses

The test of a difference in probability of recruitment of senior and junior fledglings (of known sex) of cohort 1989 was capable of detecting correlations as small as $r^2 = 0.02$. In the eight nonsignificant tests of differences in reproductive performance of senior and junior chicks, the minimal sample sizes required to detect significance were on average 870 times (range = 3 to 4,367 times) greater than our sample sizes, which varied from 183 to 434 ($\bar{X} = 343$). In the six nonsignificant tests of a difference in size between senior versus junior fledglings or recruits and the four nonsignificant tests of a relationship between size of recruits at fledging and performance on the first reproductive attempt, the minimal sample sizes required to detect significance were on average seven times (range = 1.4 to 13 times) greater than our sample sizes, which varied from 139 to 311 ($\bar{X} = 212$). Finally, for the eight nonsignificant tests of differences in broodmate pairs,

Table 4: Mean laying date, summed absolute brood sizes, and total absolute nest success during the first 10 yr after fledging of 92 senior and 91 junior recruits from broods of two in cohort 1989

Variable	df	Laying date		Brood size		Nest success	
		F	P	F	P	F	P
Seniority	1	5.17	.002	1.27	.26	1.49	.22
Sex	1	.23	.63	.15	.18	.001	.97
Seniority × sex	1	.10	.75	.007	.93	.23	.63

Note: Laying dates were centered. Five birds were not included in the analysis of laying date because their dates were unknown.

Table 5: Reproductive performance of pairs of broodmate recruits over three timescales

Variable	N	Value ($\bar{X} \pm SE$)		Seniority		Sex composition		Interaction	
		Seniors	Juniors	F	P	F	P	F	P
First reproduction:									
Age	81	4.24 \pm .14	4.37 \pm .16	.32	.57	1.44	.23	.49	.69
Brood size	81	.80 \pm .08	.95 \pm .09	1.40	.23	.95	.42	1.62	.18
Nest success	81	.53 \pm .08	.62 \pm .08	.55	.46	.79	.50	1.33	.26
5 yr:									
Summed brood sizes	81	1.20 \pm .12	1.60 \pm .15	4.01	.04	2.15	.09	1.22	.30
Total nest success	81	.82 \pm .11	1.14 \pm .13	3.42	.06	1.50	.21	1.25	.29
10 yr:									
Summed brood sizes	52	4.38 \pm .43	5.05 \pm .43	1.16	.28	.14	.93	.53	.66
Total nest success	52	3.13 \pm .35	3.67 \pm .34	1.14	.28	.57	.63	.18	.90

Note: Age (years), brood size (number of chicks), and nest success (number of fledglings) were analyzed using two-way ANOVAs (seniority \times sex composition) with split-plot design and matched subjects on brood.

detection of significant differences between seniors and juniors would have required samples on average five times (range = 1.1 to 12 times) larger than our samples, which varied from 94 to 920 ($\bar{X} = 234$). Hence, our nonsignificant results give some confidence that the corresponding differences between senior and junior chicks in recruitment and reproductive performance over periods up to 10 yr are very small or account for an extremely small proportion of total variance.

Discussion

Two variables with major and multiplicative effects on recruitment and reproductive performance were year of birth and hatch date within season. Cohorts of fledglings varied nearly threefold in probability of recruitment (from 0.21 to 0.59); cohorts of fledglings that recruited varied in first laying date, first brood size, and mean laying date over the first 5 yr but not in summed brood sizes or total nest success (both variables centered) over the first 5 yr of life. The causes of this variation among cohorts undoubtedly include interannual variation in weather, ocean temperature, and, critically, abundance of fish prey (e.g., Schreiber and Schreiber 1984; Ruiz and Lyle 1992), factors that will be analyzed in a future study. Just as striking was the finding of steeply diminishing prospects for recruitment when chicks fledged later in the season. Late fledging entailed a reduction of up to 63% in the probability of ever reproducing, although in some cohorts, the effect was absent. It is plausible that late-nesting adults are inexperienced or inferior birds that produce less viable offspring, but it seems likely that feeding conditions around Isla Isabel deteriorate as the season progresses because ocean surface temperature by the island typically increases by roughly 5°C between April, when most chicks fledge, and July, when the last few individuals fledge (García Cerecedo

and Saavedra Sordo 1997). Importantly, once recruited, late fledgers performed just as well as did early fledgers in their first reproductive attempt.

Although dominant boobies survive better than do juniors during infancy, overall, their advantage seems to end at fledging. In a sample of 190 broods of two hatchlings observed until fully feathered (Torres and Drummond 1997), seniors outsurvived juniors by 88% versus 81% (males) and 87% versus 74% (females). In our study of fledglings, overall recruitment of seniors (41%) and juniors (37%) from the five cohorts did not differ significantly, and the only advantage of dominants was their superior recruitment in two cohorts. Moreover, we probably underestimated the relative recruitment of juniors because fledglings of four cohorts entered our samples at an age (70 d) when parental feeding and differential mortality of junior chicks persist (Drummond et al. 1991). Superior recruitment of dominants in the two cohorts with the poorest recruitment may imply that dominants are better than are subordinates at dealing with a severe environmental or social challenge, but the putative challenge is unidentified and might have arisen in the natal season or during the first few years of life. Conversely, when broodmates cohabited throughout infancy, an advantage of subordinate status was indicated by juniors being less prejudiced by late fledging than were seniors. For both senior and junior fledglings, lengthy cohabitation with a broodmate was associated with reduced probability of recruiting, which implied that cohabitation with either a dominant or a subordinate broodmate incurs a roughly similar recruitment cost. Since length of cohabitation was not related to size at fledging, cost may be imposed by the social experience of cohabitation rather than an effect on growth.

In our original, large sample, seniors and juniors that successfully recruited into the breeding population per-

Table 6: Laying date of pairs of broodmate recruits at first reproduction and mean laying date during first 5 yr and first 10 yr after fledging

Sex composition	N	Value ($\bar{X} \pm SE$)		Seniority		Sex composition		Interaction	
		Seniors	Juniors	F	P	F	P	F	P
First reproduction				.44	.51	.54	.65	3.18	.02
Male-male	18	20.48 \pm 9.68	-4.01 \pm 7.66						
Male-female	14	9.53 \pm 7.32	-3.09 \pm 8.73						
Female-male	16	-12.11 \pm 6.55	10.23 \pm 7.71						
Female-female	8	1.87 \pm 10.19	-12.02 \pm 8.98						
5 yr				2.06	.15	.83	.47	3.55	.01
Male-male	16	17.66 \pm 9.71	-9.43 \pm 7.42						
Male-female	17	1.38 \pm 5.68	-9.70 \pm 5.39						
Female-male	14	-5.92 \pm 6.97	15.14 \pm 7.13						
Female-female	8	1.87 \pm 12.19	-12.02 \pm 11.33						
10 yr				3.05	.08	.21	.89	1.15	.33
Male-male	14	1.71 \pm 6.32	-14.41 \pm 4.13						
Male-female	12	-4.03 \pm 5.36	-12.45 \pm 3.96						
Female-male	13	-11.11 \pm 4.50	-7.98 \pm 5.96						
Female-female	8	-8.09 \pm 9.02	-13.04 \pm 6.37						

Note: All variables were centered. Tested with two-way ANOVAs (seniority \times sex composition) with split-plot design and matched subjects on brood. Female-male = female with younger brother.

formed similarly at reproduction. Although subordinate adults of many species establish themselves relatively late on breeding grounds (Gauthreaux 1978), junior boobies established their clutches an average 7 d earlier than did seniors over the first 10 yr of life. This advantage did not translate into (significantly) increased reproductive success as measured in this study but may have been important; offspring that fledge earlier have higher reproductive value because early fledgers are more likely to recruit (this study). Moreover, although pairs of sibling fledglings did not differ in reproductive success over the first 5 yr of life, when both fledglings recruited, juniors actually produced larger broods than did their own senior siblings over the first 5 yr of life. Hence, results from both the complete sample and the samples of pairs of broodmates imply that after fledging, subordinates have a reproductive value that at least equals and may even exceed that of dominants.

Overall, these results imply that former dominants and subordinates that survive to breed differ little if at all in their attractiveness, ability to compete for and defend resources (mates and nest sites), abilities involved in parental investment and parental care, and survival and foraging skills. However, three caveats are in order. First, it is plausible that subordinates do indeed suffer deficits in some behavioral domains but that these are compensated by use of alternative tactics (Summers 1999) or by alternative strengths in other domains. Second, it is possible that male seniors achieve greater reproductive success than do juniors (or vice versa) not in their own nests but through extrapair paternity. Third, the apparent equivalence of dominants and subordinates could partly be due to weak

junior nestlings succumbing to broodmate aggression before fledging and thereby being deleted from the sample of fledglings. There are no observations that support (or contradict) any of these suggestions, but the notion of alternative tactics or strengths seems consistent with variation in relative recruitment of seniors and juniors from different cohorts.

Both behavioral and morphological development of blue-footed boobies appear to be buffered successfully against the twin challenges that predictably confront junior broodmates: violent domination and early food deprivation. If exposure to violence and domination do indeed threaten an infant bird's development, then boobies have evidently evolved to overcome that challenge substantially or completely. Moreover, the subordinate fledglings' superior performance on some measures could plausibly be due to developmental gains that result from confronting and dealing with hostility throughout infancy. Dominants apparently reap no developmental benefits over the longer term from the exercise of aggressive control during infancy, and their underperformance in some aspects of adult reproductive life could mean that they eventually pay a cost of their daily investment in aggression, just as exercising dominance can prove costly for adult vertebrates (Pusey and Packer 1997). Junior booby nestlings are routinely starved during the first 3–4 wk of life, when they receive about 17%–29% less food (by mass) than do seniors and weigh about 11%–13% less than do seniors (Drummond et al. 1986; Guerra and Drummond 1995; and see Anderson and Ricklefs 1995), with females more affected than males (Drummond et al. 1991; and see Torres and Drum-

mond 1997). However, before fledging, juniors catch up in linear growth attainment (this study) and maximum mass (Drummond et al. 1991). Infant birds and mammals that suffer nutritional deficits early in development may pay the cost of the early deficit or subsequent compensatory growth later on during adulthood, for example, in terms of body size or morphology, survival, dominance rank, ability to acquire a territory, and fecundity (Richner et al. 1989; Richner 1992; Metcalfe and Monaghan 2001; Lumma and Clutton-Brock 2002). However, in our dependent variables, at least, there was virtually no evidence of such effects in boobies.

Three studies of avian species with broodmate aggression have shown inferior performance after fledging of chicks that were low in the brood hatching order, but in every case, the effect could have been due to inferior body size at fledging rather than the experience of aggressive subordination per se. Last-hatched kittiwake (*Rissa tridactyla*) fledglings were less likely to recruit than were first- and second-hatched fledglings, but last-hatched fledglings grew more slowly during the nestling period, and weights were not measured at fledging (Coulson and Porter 1985). Little egrets of high rank within the brood showed relatively high breeding success in later seasons (Thomas et al. 1999), but in this study, rank was based on size just before fledging (measured on the same day for the whole brood), and neither fledging size nor hatch order was known. Male black kite fledglings of low hatch rank dispersed further than did males of high rank, and Forero et al. (2002) suggested that this difference could be due to inferior competitive abilities acquired during the intense sibling aggression of the nestling period (Viñuela 1999). This is currently the best evidence for a long-term effect of dominance-subordination during the nestling period, but the authors were not confident that low-rank chicks were as large as high-rank chicks at fledging (and greater dispersal distance was not associated with inferior performance on any measure of reproduction including lifetime reproductive success). Chicks that are low in the broodmate hatching order often grow poorly and survive poorly after fledging even in species with no broodmate aggression (e.g., reviews in Spear and Nur 1994; Dittmann et al. 2001), so it would be premature to infer from any of the above studies that dominance-subordination among broodmates itself produced long-term effects on behavior.

In principle, two types of long-term behavioral effects of interactions among vertebrate broodmates and littermates seem plausible: general effects and sib-specific effects. Previous interaction with a sibling could reduce an individual's viability and competitiveness in general, such as by curtailing its aggressiveness, or it could limit the individual's competitiveness only in relation to the sibling itself by establishing a dominance relationship involving

individual recognition and an element of inertia. In our study, only general effects would be detectable because the pattern of natal dispersal in the booby colony (Osorio-Beristain and Drummond 1993) probably results in little opportunity for interaction with former broodmates during adult life (unless broodmates seek each other out). We found scant evidence of any general long-term negative effect even in a species in which the infant relationship is particularly violent, clear cut, and stable. Similarly, a review of sibling effects on human behavioral development concluded that while sib-specific effects may well be present, general effects seem to be absent. "The patterns of behavior that are acquired in sibling relationships neither help us or hinder us in our dealings with other people. They leave no permanent marks on our character" (Harris 1998, p. 61; but see Sulloway 1996).

We should look for sib-specific effects by testing for long-term behavioral consequences of sibling dominance in species in which broodmates and littermates sustain close associations into adult life (cf. Geist 1978). In numerous mammalian species, such as some canids, pigs, mongooses, and hyenas, and avian species, including some anatids, tetraonids, and phasianids, siblings belong to the same social group during at least part of adulthood. In mammals, associations of adult sisters are particularly common. If infant dominance relationships show the inertia that has often been proposed, it is in such species that early social experience with siblings may have the most enduring effects on behavior and reproductive success. The challenge will be to distinguish effects of behavioral interactions during infancy from effects of genetical and prenatal developmental differences, particularly in mammals and in birds with offspring that hatch synchronously.

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