

72 hours, the length of the cell cycle in hybrid cells between BS and normal or between BS and HBS cells appeared to be similarly expanded.

Metaphases of hybrid cells contained one diploid set each of BrdU-labeled and unlabeled chromosomes, indicating that hybrid cells between BS and normal or HBS lymphocytes reached mitosis after one complete DNA replication cycle subsequent to fusion. Further evidence of a genome of BS origin in the hybrids was established by the presence of a Y chromosome (Fig. 1). All the hybrids between BS and normal or HBS cells had a normal SCE incidence (Table 1 and Fig. 1). As shown in Table 1 (experiments 9, 10, and 11), no significant change occurred in the SCE frequencies when hybrids were produced between cells of the same origin. Thus, the process leading to normalization of SCE frequencies of BS chromosomes in hybrids with normal or HBS cells is not fusion per se or fusion-associated expansion of the cell cycle.

Although chromosomal instability and high SCE frequencies in BS cells (1, 2) may reflect a deficiency in DNA repair function (3–5), no such defect has been demonstrated. Furthermore, findings incompatible with the concept of recessive mutation in BS, that is, that a substance produced by BS cells in culture can increase SCE in normal lymphocytes, have been reported (11). Other investigators have reported that cultivation of BS with normal cells leads only to decreased SCE in BS cells (9, 10).

Cell fusion experiments have been used by some workers to study the mechanism of SCE genesis in BS cells. Even though normalization of SCE frequencies was observed in the hybrids between BS and normal cells, the possibility that segregation of a particular population of hybrid cells during the long-term culture (10 to 20 days) might have taken place was not ruled out. The issue was further complicated by the finding (8) that the SCE in BS cells can be normalized by fusing BS cells with mouse tumor cells (L-A9) that show a high SCE incidence; thus, a certain metabolic shift might well have taken place and suppressed SCE.

We used fresh normal and BS lymphocytes and the cells of a BS patient who showed no bimodality with respect to SCE frequencies in his lymphocytes and analyzed the SCE incidence in mitotic cells immediately after fusion to circumvent some problems of other fusion experiments (6–8). The results demonstrate that the normalization of SCE in BS cells occurred in euploid cell hybrids after

only one round of DNA replication subsequent to fusion. Since the HBS cells also corrected the BS defect as effectively as did normal cells, it appears that BS is, as expected, a result of a recessive homologous mutation.

Since correction of the SCE defect in BS cells can be achieved by fusion with cells of several species (6–8), our results suggest the presence of a factor in the cells of several species that is capable of correcting the defect responsible for the high SCE frequencies in BS cells, rather than the production of a DNA-damaging substance by the BS cells (14). The absence of such a factor in the BS cells leads to the high SCE frequencies.

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Increased Reproductive Effort with Age in the California Gull (*Larus californicus*)

Abstract. Comparisons of reproductive behaviors of three age classes of California gulls demonstrate that reproductive effort increases with age in this seabird. These findings contradict the assumption that increased reproductive success with age results from increased experience and social status and demonstrate that selection for increased reproductive effort can occur in long-lived species.

Several theoretical considerations have both supported (1, 2) and refuted (3–6) Williams's (7) hypothesis that long-lived organisms increase their reproductive efforts with age. However, there is a dearth of behavioral data on the topic. I report here that the reproductive efforts (risks taken and energy expended) of the California gull increase with the age of the parents.

The breeding site under study is on an island 24 km west of Laramie, Wyoming, in the Bamforth Lake Wildlife Preserve. Gulls in the colony have been banded yearly since 1959 (8); there are now more than 1000 banded gulls in a population of over 4000. To permit accurate mapping of the individual nests, the site was divided into a grid system, with metal stakes as reference points. The wings of 39 banded gulls were specially marked, and others were identified by the numbers on their leg bands. A sample of 21 pairs of young gulls (3 to 5 years old), 20 pairs of middle-aged gulls (7 to 9 years old), and 18 pairs of old gulls (12 to 18 years old) was obtained from previous

banding records. The nests of these birds were marked with numbered stakes. Gull behavior was observed from a 15-foot observation tower.

Reproductive success was determined by counting the number of surviving chicks fledged by each pair throughout the breeding season. Data were also collected on the number of times offspring were fed, the number of acts of territorial defense, and the amount of time each parent spent on the nest during 437 1-hour observation periods (9) standardized for the time of day and the age of chicks when measurements were taken. The data were compared between age classes and on the basis of whether the nest was located in the center of the colony or the periphery. In comparing locations, equal numbers of parents from each age class were analyzed for each location. The behavior of parents while off the nest was also observed, with daily checks for marked birds on the beaches adjacent to the breeding colony. Finally, 420 observations of the foraging behavior of gulls were made at five lakes and

from various roadside locations on the Laramie Plateau.

Reproductive success increased with the age of the parents (means: young parents, 0.76 ± 0.22 ; middle-aged parents, 0.80 ± 0.17 ; old parents, 1.5 ± 0.20) [two-way analysis of variance, $F(2, 53) = 4.24$, $P < .02$]. Within age groups, there were no significant differences between reproductive success at central and peripheral nest locations, nor were there significant interactions between age and location. Proportionately, however, more old gulls occupied central nest sites [$\chi^2(1) = 4.75$, $P < .05$].

Observations of gulls away from the colony yielded 391 cases of gulls actively foraging and 29 cases of gulls in flight to or from the colony. None of the gulls were seen resting while they were away from the colony. The beach was checked daily for actively nesting birds, but none were seen. All the marked birds observed in beach areas had failed to breed or had not attempted to breed. I concluded that the amount of time spent away from the nest site was a reliable indicator of the amount of time spent foraging. The amount of time both parents spent on the nest was highest in young gulls [$F(2, 36) = 164.40$, $P < .001$] (Fig. 1A).

Parents generally alternated between foraging trips and nest guarding. One parent guarded the nest, leaving to forage when its mate returned. Sometimes the guarding parent did not wait for its mate to return and left the nest unattended. This behavior occurred with increased frequency as chicks approached fledging age and was negatively correlated with offspring feeding rates ($r = .66$, $P < .001$). Young parents were most likely to leave their chicks unattended, and did so for the longest periods [Kruskal-Wallis one-way analysis of variance, $H(2) = 7.92$, $P < .02$] (Fig. 1A).

Old gulls fed their chicks most frequently [$F(2, 37) = 6.06$, $P < .01$] (Fig. 1B), and did not reduce the frequency until their chicks were more than 35 days old—5 days longer than the period of maximum frequency accorded the chicks of younger parents. The number of acts of territorial defense also increased with the age of the parents [$F(2, 37) = 3.51$, $P < .05$] (Fig. 1B). Nest location did not significantly influence any of the behaviors measured.

Increased reproductive success of older individuals in populations of seabirds has been attributed to experience and social status (10–12). Experience has yet to be quantified in adult seabirds; however, old gulls may feed their offspring more frequently because of greater for-

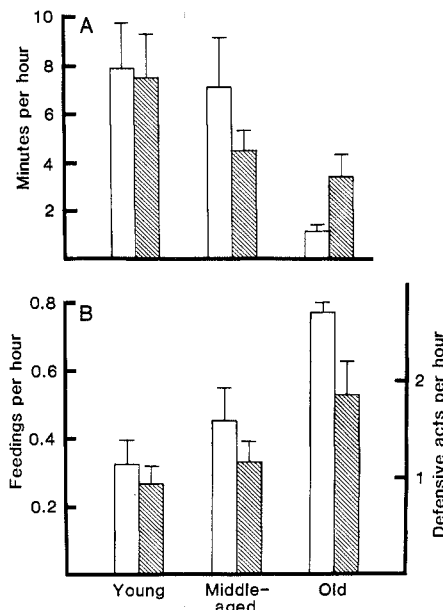


Fig. 1. Duration and frequency of behaviors measured at the nesting site (means $\pm$ standard errors). (A) Time during which nest was unattended by parents (open bars) and during which neither parent foraged (shaded bars). (B) Frequency of offspring feedings (open bars) and frequency of acts of territorial defense (shaded bars).

aging ability. Experience does not explain the smaller amounts of time during which neither parent foraged and the longer duration of offspring feedings (13). Furthermore, it is doubtful that there exists a learning process, lasting upward of 9 years, that increases reproductive success. Rather, increased reproductive effort is the most parsimonious explanation.

Some investigators have found higher reproductive success among birds nesting in the central areas of colonies and have concluded that the center represents a socially advantageous breeding position (12). This study indicates that there are no such differences. The only difference between central and peripheral areas was the ages of the nesting gulls. Considering that old gulls have the highest reproductive success, observations of higher reproductive success in the center of a colony can be explained by age differences alone.

Old gulls expend more time and energy than younger gulls in territorial defense, foraging, and parenting. Territorial defense clearly increases risks of injury and death to the defender. Additional foraging by old gulls can be postulated as incurring further risk, since injury is more likely to occur in foraging than in resting. Because of the mobbing behavior of the gulls, adults are probably safer from predation while resting in the breeding colony [the fact that resting

gulls (including nonreproducing ones) were always found in or near the colony supports this hypothesis]. However, as we have seen, old gulls have less time available to spend in the colony than younger birds. Their greater energetic output may weaken them, and thus result in increased susceptibility to disease and predation, or inability to complete the return migration to California. The comparative increase in reproductive efforts by old gulls coincides closely with observed increases in reproductive success.

The cost of reproductive effort can be measured in terms of loss of future reproductive success (1). Energetic investments and risks of mortality incurred by current reproductive efforts decrease the probability of future reproductive success. As an animal grows older, the cost of reproductive effort grows smaller because the animal has fewer breeding opportunities remaining (expected future success is small). The life history of long-lived animals is such that strenuous reproductive efforts early in their lives may be too costly to justify the benefits. Therefore, long-lived animals may be selected for reproductive restraint while they are young and increasing reproductive effort as they grow older. Increased reproductive success with age reported for many species of seabirds (14–17) may be a result of similar selective pressures.

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