Behav Ecol Sociobiol (1987) 21:217–221

Behavioral Ecology and Sociobiology

Age-specific survivorship in relation to clutch size and fledging success in California gulls

Bruce H. Pugesek *
Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA

Received October 2, 1986 / Accepted June 22, 1987

Summary. Data from a natural population of California gulls (*Larus californicus*) demonstrated that increasing reproductive effort with age was associated with reduced survivorship. Number of offspring fledged but not clutch size was inversely related to adult survivorhip indicating that reproductively induced mortality resulted from the cumulative effects of the entire breeding season. Age-related increases in fledging success were correlated with increased adult mortality. Young gulls fledged few offspring and had high survival rates. Old gulls tended to fledge more offspring and had low survival rates. However, those old gulls fledging few offspring survived as well as young gulls. Data also invalidate the assumption that survivorship is age-constant in this species.

Introduction

The idea that reproductive effort should increase with age, first proposed verbally by Williams (1966a, b), has been rigorously formulated by a number of authors (Gadgil and Bossert 1970; Schaffer 1974; Pianka and Parker 1975; Charlesworth and Leon 1976; Michod 1979). These models assume tradeoffs in which current reproductive effort reduces future reproductive potential. Current reproduction may reduce energy available for somatic maintenance and growth which may in turn reduce future fecundity. Current reproduction may also reduce survival to future breeding opportunities. The optimal level of reproductive effort should increase as individuals age and the potential for future survival declines.

Behavioral data on California gulls (*Larus californicus*) support the hypothesis of increasing reproductive effort with age. Older gulls defend and forage for their offspring more frequently and over a longer duration of parental care compared to younger gulls. Fledging success increases with age in association with increased reproductive efforts (Pugesek 1981, 1983).

Such increases in reproductive effort should result in reduced potential for future reproduction. Gulls are determinant growers, therefore, energy invested in current reproduction does not reduce future fecundity by reducing growth. For gulls, the tradeoff for high current reproductive effort should be reduced survivorship.

To date, I have provided evidence that behavioral acts such as defense of offpring may result in adult mortality and that older gulls have significantly higher mortality on their breeding island compared to younger gulls (Pugesek 1983). Older gulls also lose significantly greater amounts of body weight during the breeding season compared to younger gulls (Pugesek 1984). Such weight loss may result in mortality after the breeding season.

Here I present data on survivorship of the population of gulls for which reproductive effort and fledging success have previously been described (Pugesek 1981, 1983; Pugesek and Diem 1983). Survivorship is compared to age and previous reproductive output (clutch size and fledging success) to test the hypothesis that age-related increases in reproductive effort result in decreased survival to future breeding opportunities.

Methods

I compare levels of reproductive success in 1980 (clutch size and fledging success) of known-aged gulls with their survival measured by census in 1984. Data are from a sample of known-aged gulls (see Pugesek 1983) in the Bamforth nesting colony (Bamforth Lake, Albany County, Wyoming).

Data on reproductive success were obtained by locating banded gulls on the breeding colony during the territorial phase

* *Current address:* Department of Human Development, The Pennsylvania State University, S-210 Henderson Human Development Building, University Park, PA 16802, USA

of reproduction and marking the nest cup with a coded stake. Leg band numbers of the gulls were read and individuals aged at a later date by referring to banding records. Clutch size ($N=190$ nests) was determined during daily censuses of nests in which the number of eggs laid, including replacement eggs, were counted. Both sexes were used in comparisons of clutch size with survival. Males courtship feed females, therefore, both sexes contribute to investments in eggs (Pugesek 1983). Fledging success ($N=140$ nests) was defined as the number of offspring per nest that survived 5 weeks or more. Mean fledging success presented in results includes nests that failed to produce any offspring. Fledging success was monitored at least every 2 days from an observation tower located near the periphery of the colony. The colony was not entered once hatching began to avoid creating an artificial source of chick mortality. Fledging success of nests nearest the observation tower did not differ significantly from other peripheral areas of the colony (Pugesek and Diem 1983). Mixing of broods was not observed including 50 broods in which offspring were color banded for individual identification.

Adult survival was estimated by censusing the entire breeding colony in 1984. Banded gulls were identified, aged, and territories marked by the method described above. The breeding colony is divided by a grid system that allowed the colony to be covered repeatedly in transects. In addition, staked nests were monitored to determine whether banded gulls had banded mates and, if so, those individuals were included in the census. Most gulls (99%) were located at nesting territories, however, 2 were identified at the edge of the colony. Gulls were presumed dead in 1984 if they were not located in the census.

Gulls are known to skip breeding seasons and return to the breeding colony in subsequent years, thereby, biasing a single year census. However, this bias should be in a direction opposing the trend presented here. Young California gulls (Pugesek unpublished data) as well as kittiwakes (Wooller and Coulson 1977) are more likely to skip breeding and the tendency declines with age.

No censuses were conducted from 1981 to 1983. Strength of correlations between survival and past reproductive success are probably weakened by the gap of intervening years. However, this census method eliminates bias in correlations between reproductive success and survival produced by a tendency, if any, for gulls to skip breeding in a year following a particularly high reproductive investment.

Band loss is sufficiently low to be a minor source of bias in this study. Gulls are double leg banded; one band is made of a steel alloy material which is highly wear resistant and difficult to pull off. Judging from the number of doubly banded gulls that lost the steel band and retained the other aluminum band, loss of the steel band occurred in <1% of the sample over the course of this study. With the minimal band wear that occurs, chance of band loss within a fixed interval of time would be similar regardless of an individual's age. Comparisons of survivorship of known-aged gulls were made between the interval of 1980 and 1984 and did not depend on the amount of band loss that occurred before 1980.

Estimates of survivorship are difficult to make if individuals do not return to the same site to breed in the following years. The fidelity of gulls (in Bamforth Lake) to their breeding site is well documented. No other California gull colony exists within 80 miles of Bamforth Lake. The four California gull colonies that exist within Wyoming are all regularly observed by biologists. No gull from our sample has ever been reported to breed on these or any other colony in North America. This includes reports on over 800 band recoveries and over 500 reported sightings of more than 2000 individuals which have been marked with highly visible patagial wing tags.

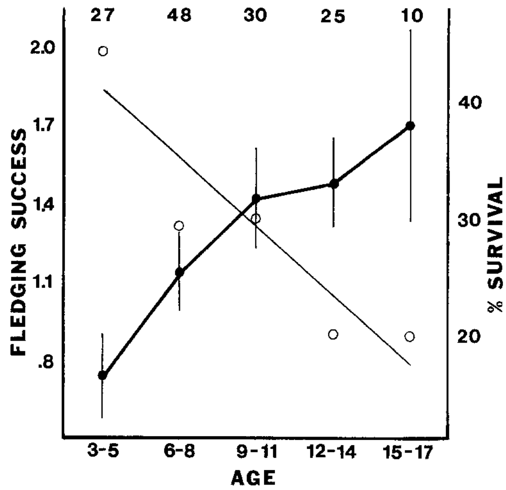

Fig. 1. Fledging success (number of offspring per nest) and % survival rate of gulls ranging in age from 3 to 17 years old. Age is divided into 3-year age groups. Mean fledging success (*solid dots*) ±SE for each age group is connected by the *thick line*. The *thin line* plots the regression for % survival (*open dots*) with age. Sample sizes for each age group are 27, 48, 30, 25, and 10 respectively

Regression, analysis of variance, and analysis of covariance statistics were calculated using SAS, and contingency analyses were calculated by hand. Data were tested for and conformed to assumptions of the various statistical tests used (Sokal and Rohlf 1969).

Results

Fledging success increased significantly as a function of parental age (Fig. 1, Table 1a). Survivorship of adults declined continuously as a function of age. Birds, 3–5 years old had the highest survival rate (44%) while only 20% of birds 12 and older survived to 1984. Regression analysis showed that percent survival decreased with age with a slope significantly different from zero ($r^2=0.84$; $P<0.05$, regression equation: $y=48.5-1.93\,X$) (Table 1b).

In order to determine whether increased mortality resulted solely from age or level of reproductive effort, levels of breeding success (clutch size CS, and fledging success FS) were compared between survivors and nonsurvivors (Fig. 2). Data were divided by age into two age groups similar to those on which behavioral data has been previously published: young gulls (3–10 years old) which expended low effort and had significantly lower clutch size and fledging success were compared to old gulls (11–17 years old) which expended the highest levels of effort.

Adult survival did not depend on the number of eggs laid. Survivors and nonsurvivors of both

Table 1. Statistics and significance levels for:
a) ANOVA – fledging success X age,
b) Regression – survival X age,
c) ANOVA – clutch size of surviving and nonsurviving young gulls,
d) ANOVA – clutch size of surviving and nonsurviving old gulls,
e) ANOVA – fledging success of surviving and nonsurviving young gulls,
f) ANOVA – fledging success of surviving and nonsurviving old gulls,
g) ANOVA – fledging success of surviving and nonsurviving old gulls with age covariate

Source	*df*	*F*	*P*
a) Age	4	3.00	0.02
Error	135		
b) Explained	1	15.91	0.05
Unexplained	3		
c) Survival	1	0.45	0.51
Error	113		
d) Survival	1	0.04	0.84
Error	73		
e) Survival	1	0.47	0.49
Error	86		
f) Survival	1	5.87	0.02
Error	50		
g) Survival	1	5.76	0.02
Age	1	0.03	0.87
Error	49		

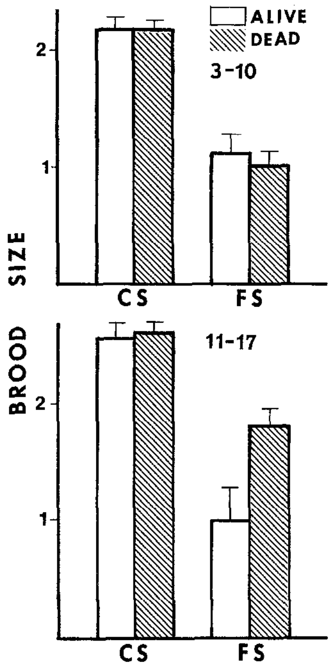

Fig. 2. Means ±SE of brood size of survivors (*open bars*) and nonsurvivors (*hatched bars*). Data for clutch size (*CS*) and fledging success (*FS*) are presented for young gulls (3–10 years old) and old gulls (11–17 years old)

age groups differed little with respect to clutch size (Fig. 2, Table 1c, d).

Young gulls (3–10 years old) fledged few young. Not surprisingly, adult survival in this age class did not correlate with offspring production (Fig. 2, Table 1e). However, out of six young gulls that fledged 3 offspring only one survived to 1984.

Older gulls exhibited a wider range of levels of fledging success. In this group, those with high fledging success were less likely to survive. Those individuals which survived had low fledging success ($\bar{X}=1.0$ per nest) similar to that of young gulls (Fig. 2). Nonsurvivors had significantly higher fledging success ($\bar{X}=1.8$ per nest) (Fig. 2, Table 1f).

Analysis of covariance was performed on the fledging success of the old group as a function of survivorship using parental age as a covariate. Results indicated that survivorship was significantly related to fledging success after holding variation in parental age constant (Table 1g). Mean fledging success of survivors and nonsurvivors adjusted for the age of parents were the same as those presented in Fig. 2. Age of parents did not alter this relationship. Mean age of survivors (12.6 years old) and nonsurvivors (12.1) were nearly identical. Therefore, the number of offspring an individual reared rather than its age determined survival among older gulls.

Age, fledging success, and survival were also compared by contingency analysis. Few young parents (3–10 years old) had large broods. Therefore, all fledging success levels of this group are lumped into one category. Their survival rate (31 of 88: 35%) is compared to that of older gulls (11–17 years old) which had 0 or 1 fledgling (9 of 23: 39% survival) and 2 or 3 fledglings (2 of 29: 7%) survival. Older gulls which fledged 0 or 1 offspring had slightly higher survival than young gulls: the difference between the two groups was not significant ($\chi^2_1=0.62$; *NS*). Those older gulls which fledged 2 or 3 offspring had significantly lower survivorship than either young gulls ($\chi^2_1=7.98$; $P<0.01$) or old gulls fledging 0 or 1 offspring ($\chi^2_1=8.02$; $P<0.01$). The lower survival of the oldest members of the population occurs primarily as a result of the high cost of fledging 2 or 3 offspring.

Discussion

Age-related increases in fledging success correlate with decreasing adult survival. Young gulls fledge few offspring and have high survival rates. Old gulls survive less well because fledging success tends to be high. However, those old gulls fledging few offspring survive as well as young gulls. Thus, data support the prediction that high reproductive effort reduces future reproductive potential through decreased survivorship.

Correlations between survival and fledging success may be influenced by the number of breeding seasons gulls skipped from 1981–1983. Young gulls skip breeding more frequently than older gulls and this behavior greatly improves chances for survival (Pugesek and Diem, in preparation). However, if the relationship between age-related decline in survival and fledging success is due to covariation with skipping behavior, clutch size should also be correlated to survival. Clutch size is not related to survival and it therefore appears less likely that correlations between fledging success and survivorship occurred due to covariation with another age-related factor.

In 1979 and 1980, 47 adult mortalities occurred on the breeding island amounting to $\simeq$ 1% of the breeding population each year (Pugesek 1983). Such mortality occurs primarily among older gulls as a result of fighting (Pugesek 1983). I was unable to monitor most deaths that occurred away from the breeding island. However, few one-parent nests were observed and it would seem that adult mortality was low during the breeding season. If adults succumb during the last days of the breeding season, deaths may go undetected. Offspring are capable of flying at this time, and leave the nest when parents fail to return. It is impossible, therefore, to determine whether a parent's absence means that it died or whether it had completed fledging its offspring.

Results indicate that the main source of reproductively induced mortality occurs after offspring are fledged as a result of the cumulative effects of an entire breeding season. Clutch size does not correlate with survivorship. Winkler (1985) obtained a similar result comparing clutch size and survival between two populations of California gulls. In such a species with protracted parental care, the number of eggs laid is perhaps a negligible portion of the overall breeding effort and may not itself critically affect survivorship. However, the stress of rearing several large offspring may accumulate and may only become critical to survival at the end of the breeding season. Both sexes lose weight continuously through the reproductive cycle (Pugesek 1984; Pugesek unpublished). Older gulls lose significantly greater amounts of weight during the breeding season compared to younger gulls (Pugesek 1984). Higher weight loss among older gulls is presumably a result of rearing larger broods, greater apportionment of food to offspring, and longer durations of parental care (Pugesek 1983). High weight loss may contribute to adult mortality by decreasing gulls' abilities to withstand disease, avoid predation, or complete the migration to their wintering grounds on the Pacific Coast. It is unlikely that high weight loss is an adaptive mechanism that reduces energy demands of migration. Gulls that lose high amounts of weight are weak, easily fatiqued, and fly with difficulty.

Results demonstrate reproductive costs among older gulls (11–17) in terms of increased mortality. Few young gulls (3–10) had large broods, therefore, sample size was not sufficient for comparison within younger age classes. The survival rate of young gulls was comparable, however, to old gulls with similarly small broods.

Some investigators (e.g. Nur 1984) follow the assumption that survivorship is age-constant. These results provide an additional exception to this assumption. In kittiwakes, decreasing survivorship occurs concomitantly with age-related increases in breeding success (Wooller and Coulson 1977). Individuals that begin breeding at 4-years-old have lower survival rates compared to those that begin breeding at 5-years-old or more (Coulson and Wooller 1976). Therefore, age-related increases in mortality among kittiwakes may also result from costs associated with reproductive effort. Seabirds, as a rule, increase fledging success with age (many examples in Ryder 1980). If such increases in fledging success are due to increased reproductive effort, survivorship should also decline with age in these species.

In a correlational study such as described here, it is difficult to assess cause and effect (Reznick 1985). Some additional covariate of reproductive effort may be responsible for age-related increases in mortality. Correlational results presented here are, however, useful in demonstrating that a life history pattern of increasing reproductive effort with age, predicted on the basis of tradeoffs between current and future reproductive potential, occurs in a naturally reproducing population.

Acknowledgements. I would like to express my thanks to Richard D. Howard for his comments on the analysis of data and writing of this paper; Kerry Rabenold for discussions on the theory of reproductive effort; Bethia Hurlbutt, Richard B. King, Hans Landel, Peter Waser, and Scott Wissinger for editorial comments. Special thanks are due Kenneth L. Diem for sharing his data on the Bamforth gulls and Richard Guenzel for invaluable assistance in the field. Research was supported by NSF grant DEB-7911557, Sigma Xi, The Wilson Ornithological Society, and The Chapman Foundation.

References

Charlesworth B, Leon JA (1976) The relationship of reproductive effort to age. Am Nat 110:449–459

Coulson JC, Wooller RD (1976) Differential survival rates among breeding Kittiwake Gulls, *Risa tridactyla* (L.). J Anim Ecol 45:205–213

Gadgil M, Bossert W (1970) Life historical consequences of natural selection. Am Nat 104:1–24

Michod RE (1979) Evolution of life histories in response to age-specific mortality factors. Am Nat 113:531–550

Nur N (1984) Increased reproductive success with age in the California gull: due to increased effort or improvement of skill? Oikos 43:407–408

Pianka ER, Parker WS (1975) Age-specific reproductive tactics. Am Nat 109:453–464

Pugesek BH (1981) Increased reproductive effort with age in the California Gull (*Larus californicus*). Science 212: 822–823

Pugesek BH (1983) The relationship between parental age and reproductive effort in the California Gull (*Larus californicus*). Behav Ecol Sociobiol 13:161–171

Pugesek BH (1984) Age-specific reproductive tactics in the California gull. Oikos 43:409–410

Pugesek BH, Diem KL (1983) A multivariate study of the relationship of parental age to reproductive success in California Gulls. Ecology 64:829–839

Reznick D (1985) Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267

Ryder JP (1980) The influence of age on the breeding biology of colonial nesting seabirds. In: Burger J, Olla BL, Winn HE (eds) Behavior of marine animals, Vol 4. Marine birds. Plenum Press, New York

Schaffer WM (1974) Selection for optimal life histories: the effect of age structure. Ecology 55:291–303

Sokal RR, Rohlf FJ (1969) Biometry. Freeman, San Francisco

Williams GC (1966a) Adaptation and natural selection: a critique of some evolutionary thought. Princeton University press, Princeton, NJ

Williams GC (1966b) Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–692

Winkler DW (1985) Factors determining a clutch size reduction in California gulls (*Larus californicus*): A multi-hypothesis approach. Evolution 39:667–677

Wooller RD, Coulson JC (1977) Factors affecting the age of first breeding of the Kittiwake *Rissa tridactyla*. Ibis 119:339–349