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Parental effort in the California gull: tests of parent-offspring conflict theory

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Summary. Parental effort was studied among known-aged California gulls (*Larus californicus*) with a brood size of two. Results supported three of Triver's predictions from parent-offspring conflict theory. First, the amount of time parents withheld food from offspring increased with increasing offspring age. Second, older parents were less likely than younger parents to withhold food from offspring throughout the period of parental care. Third, older parents had a longer period of parental care compared to younger parents. Adult survival to future breeding seasons was inversely related to duration of parental care. Older parents, in association with their greater levels of parental effort, had a lower survival rate compared to that of younger parents.

Introduction

Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Conflict should occur when the level of investment of the parent, selected to maximize its future reproductive success, is lower than the level of investment required by the offspring to maximize its own reproductive success.

Trivers (1974) demonstrated in theory that such conflict should be expected throughout the period of parental care and may become evident in the situations such as feeding when parents may elect to withhold food in spite of begging from offspring. As offspring grow and require greater amounts of food, parents may themselves require more food to replenish their depleted reserves. The rising cost of such investment in current offspring should eventually lead adults to terminate parental care. Trivers, therefore, predicts that the intensity of parent-offspring conflict should increase as the period of parental care progresses. Empirical studies have shown increased conflict over food as the period of parental care nears an end (Davies 1976; Berger 1979). Budgerigars display behavioral strategies and counterstrategies consistent with parent-offspring conflicts (Stamps et al. 1985). The above studies did not demonstrate that parental behaviors (e.g., feeding) qualified as parental investment in that they reduced the parent's ability to invest in other offspring.

As parents age, potential for future reproduction should decline (Williams 1966; Gadgil and Bossert 1970; Trivers 1974; Pianka and Parker 1975; Charlesworth and Leon 1976). Therefore, the cost of reduced future reproductive success resulting from a given level of parental behavior declines with age. As a result, older parents should be selected to invest more in offspring compared to younger parents. Greater allocation of parental investment should reduce parent-offspring conflict because the higher levels of investment by older parents should correspond more closely to the survival strategy of offspring.

Trivers (1974) makes two additional predictions related to higher levels of parental investment among older parents compared to younger parents. Since conflict is predicted throughout the period of parental care, Trivers predicts that older parents should be less likely to withhold investment (e.g., food) at any point in the offspring's period of parental care. Since increasing costs to parents lead to increased conflict and the termination of parental care, Trivers predicts that older parents will have a longer period of parental care.

In this paper, differences in latency to feed offspring during the first 45 days of offspring life are compared to test the first prediction above that parent-offspring conflict increases as the period of parental care progresses. Latencies to feed are also compared between younger (3–10 years old) and older parents (11–17 years old) to test the second prediction that older parents have lower parent-offspring conflict at any point in the period of parental care. Number of days parents and offspring remain at the nest site is compared between younger and older parents to test the third prediction that older parents have a longer period of parental care. This measure of the duration of parental care is further compared to subsequent adult survival to determine whether it is

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associated with a reduced ability to invest in future offspring. Data were gathered on gulls with a brood size of two; therefore, adult mortality due to parental behavior is a measure of parental effort. Parental effort is defined as the sum of parental investment received by each offspring in a given time (Low 1978; Zeveloff and Boyce 1980). It is assumed here that Triver's predictions for parental investment hold for parental effort, given a constant brood size. Finally, survival of younger and older parents is compared to determine whether behavioral differences between the two age groups are associated with differences in survival rate.

Methods

Behavioral and fledging success data were collected in 1980 on a population of California gulls nesting on an island in Bamforth Lake, Albany County, Wyoming. Gulls foraged primarily in nearby lakes and the Laramie River and were largely dependent on natural food resources (Kennedy 1973; Pugesek 1983).

Gulls were aged from banding data. Nearly fledged chicks have been banded almost every year since 1958. The sample of known-aged adults was obtained by reading band numbers of gulls with a spotting scope as they defended nesting territories in May, and individuals were aged from banding data at a later date. The nest of each individual was marked with a coded stake (2 × 5 × 30 cm). I did not enter the colony shortly after eggs began hatching in order to avoid producing unnatural chick mortality. Number of surviving chicks was monitored at least every other day from an observation tower located on the periphery of the colony. Previous studies (Pugesek and Diem 1983) indicated that no investigator-caused bias occurred at distances greater than 35 m from the observation tower; therefore, only those nests 35 m or more beyond the observation tower were used for measures of behavior and reproductive success. Mixing of broods was not observed, including 50 broods in which offspring were color-banded for individual identification (Pugesek 1987). Chicks were considered fledged if they survived 5 weeks or more. To equalize potential benefits of current parental efforts for all parents, only data from nests fledging two offspring were analyzed. This brood size was selected because it was the most common and occurred among parents of all ages. Most of the sample came from two-egg clutches; however, six younger and six older parents had three-egg clutches. In three of these cases, one egg was lost to predation. In the remaining nine cases, a single chick died before its second day of life. No feeding latency data were analyzed from these nests until after the third chick died. No discernbile survival differences occurred between parents with two- (41% survival) and three-egg (42% survival) clutches. In previous studies of this population (Pugesek 1987) and other California gull populations (Winkler 1985), clutch size was also unrelated to survival.

Data on parental behavior were collected from the observation tower. Feeding latency was measured as the number of minutes parents waited to feed offspring after returning from a foraging trip. Data were gathered from 14 younger parents (3–9 years old) and 11 older parents (11–17 years old). No feeding latency data were collected on 10-year-olds. Observations ($N = 239$) were randomized for time of day and offspring ages. No parent was observed more than once on any given day. If feeding did not occur within 30 min after the parent returned from foraging, the observation was terminated and a value of 30 min assigned.

The termination of parental care is a gradual process involving reduced feeding and attentiveness to offspring at the nest site (Pergusek 1983). Parents eventually abandon the nest entirely and no parental care has been observed away from the nest site (personal observation). Therefore, last sightings of parents at the nest site are used here as a measure of the termination of parental care.

The duration of parental care (DPC) was measured as the period from the date of hatching of the first egg of the brood to the last sighting of parents at the nest site. Last sightings were determined by daily 3-h observations of the nest site at the end of the 1980 breeding season. Data presented here on DPC differ from that of two-chick broods published previously (Pugesek 1983) because DPC in the earlier paper was calculated from last sightings of either parent. DPC presented here was calculated from last sightings of only the known-aged parent. Data were from 18 younger parents (3–10 years old) and nine older parents (11–17 years old).

Gulls fledged at Bamforth Lake usually return to their natal site to breed, and having established a breeding site, remain faithful to it. This high degree of fidelity to the breeding area permits estimates of survival based on return rate (Pugesek 1987; Pugesek and Diem 1990).

Adult survival was estimated by censusing the entire breeding colony in 1984, 1985, and 1986. Banded gulls were identified, aged, and territories marked by the method described above. Band loss, less than 1% over the course of this study, was sufficiently low to be a minor source of bias (Pugesek 1987). The breeding colony is divided by a grid system that allowed the colony to be covered repeatedly in transects. Transects were searched in differing orders and times of day. Each yearly census was completed when no new birds were located in two consecutive searches of the breeding island. 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, six were identified at the edge of the colony. Band numbers of these individuals were easily read, usually many times, since they often moved to different areas of the colony. Therefore, it is unlikely that birds without permanent territories avoided detection. More than ony yearly census was used to estimate survival in order to locate gulls that skipped breeding in 1984. Five additional gulls were located in the 1985 census. No additional gulls were located in 1986; therefore, 2 years of census data appeared sufficient to locate survivors.

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

Samples of young and old parents used throughout consisted of approximately equal proportions of males and females. Data were tested for violations of assumptions of statistical tests performed (Sokal and Rohlf 1969) and data transformed when necessary.

Results

Feeding latency was significantly longer among younger parents compared to older parents (Fig. 1; Table 1). At all chick ages, young parents withheld food from offspring for longer periods of time. Feeding latency was high initially among parents of both age groups and declined as chicks grew and their energetic demands increased. As chicks approached fledging age, feeding latency increased for both age groups of parents (Fig. 1). At 21 days old, latencies to feed offspring reached high levels among younger parents. By the 41st day, feeding by younger parents had almost completely stopped within the observation period, indicating the termination of parental care. Older parents, however, continued to feed offspring shortly after arriving at the nest site from foraging trips until chicks were 41 days old. At 41–45 days, older parents fed their offspring with latencies similar to those of younger parents with 21- to 40-day-old offspring.

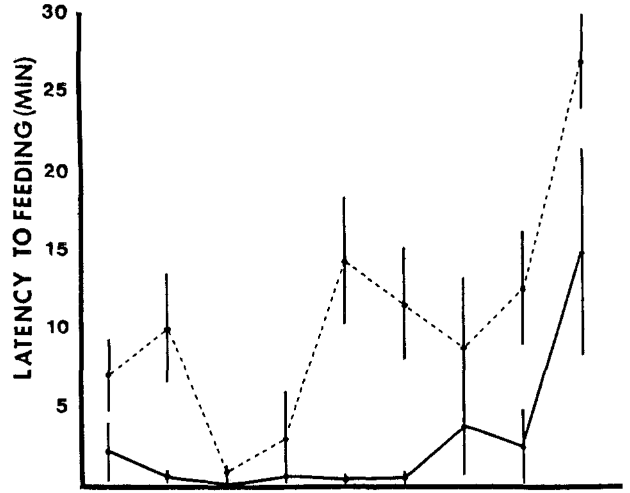

Fig. 1. Feeding latencies, the number of minutes parents waited to feed chicks after returning from foraging (means ± SE). Younger parents = 3–9 years old (dotted line); older parents = 11–17 years old (solid line). Data are partitioned into 5-day intervals, starting with the hatching of the first chick of each brood. Sample sizes were: 23, 14, 20, 6, 13, 16, 8, 15, and 6 at chick ages 0–5 through 41–45, respectively, for younger parents, and 13, 24, 18, 12, 15, 11, 9, 10, and 6, respectively, for older parents

Table 1. Two-way ANOVA table of data on feeding latencies in relation to parent age and chick age (*** indicates $P<0.001$). Variation was low among older parents at most offspring ages because they usually fed offspring shortly after returning from foraging. Distributions were also highly skewed, requiring an arc tangent transformation on feeding latencies to meet the assumptions of normality and homogeneity of variances

Source	SS	*df*	MS	F
Parent age	17.33	1	17.33	52.99***
Chick age	10.13	8	1.27	3.87***
Interaction	2.43	8	0.30	0.93$^{\mathrm{NS}}$
Error	72.30	221	0.33	

DPC was significantly longer among older parents compared to younger parents (ANOVA: $F_{1,25}=6.16$, $P<0.02$; Fig. 2a). Older parents remained at the nest site about 4 days longer on average than did younger parents.

Survival among older gulls was significantly lower compared to younger gulls ($\chi^2_1=7.43$, $P<0.01$). Only 17% of older gulls (3 of 18) survived to 1984 compared to a 57% survival rate among younger gulls (16 of 28).

Analysis of covariance was performed on DPC as a function of survival using parental age as a covariate. Results indicated that survival was significantly related to DPC with ($P<0.04$) and without ($P<0.004$) the age covariate (Fig. 2b; Table 2). DPC among survivors was on average 5 days shorter compared to nonsurvivors. Parental age had little effect on the relationship between survival and DPC. Mean DPC adjusted for the parental age covariate was similar to the true means. Therefore, DPC rather than an individual's age was related to survival.

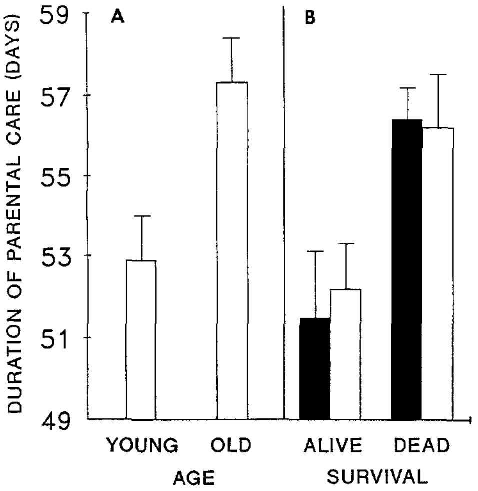

Fig. 2 A, B. Duration of parental care (means ± SE) measured for **A** younger parents (3–10 years old) and older parents (11–17 years old) and **B** parents that survived or died (dark bar = true means ± SE; open bars = means ± SE, adjusted for parental age covariate)

Table 2. Analysis of covariance table of duration of parental care among survivors and nonsurvivors with parental age as a covariate

Source	SS	*df*	MS	F	P
Survival	166.44	1	166.44	9.96	0.004
Survival with covariate	80.26	1	80.26	4.80	0.04
Age	27.76	1	27.76	1.66	0.21

Discussion

Data on latency to feed offspring support Triver's first two predictions. First, parents withhold food for greater periods of time as offspring grow older, indicating that parent-offspring conflict increases as the period of parental care progresses. Second, older parents withhold food for lesser amounts of time compared to younger parents at all offspring ages, indicating that old parents have reduced parent-offspring conflict at any point in the period of parental care.

The above conclusions assume that, by withholding food, parents increase their potential to invest in future offspring while current offspring have reduced chances of reproductive success. Data from previous studies of this population indicate that these assumptions are valid.

Adult gulls lose significant amounts of body mass as the breeding season progresses (Pugesek and Diem 1990) and this may be a primary cause of their deaths (Coulson et al. 1983; Pugesek 1987). Gulls feed offspring partially digested boluses of food. The amount of time parents withhold food from offspring is one method by which parents could control how food is partitioned between themselves and offspring. The longer food is withheld, the greater the amount that may be assimilated by the parent. Older parents withhold food less frequently, and older gulls (Pugesek and Diem 1990) lose significantly more body mass through the course of the breeding season compared to younger gulls. Declining survival with age is not related to senescence but is directly related to higher levels of reproductive effort (Pugesek and Diem 1990). Thus, the act of withholding food throughout the course of the breeding season may be one way that parents maintain their physical condition and may be directly related to adult survival for future breeding opportunities. Further investigation is required to determine whether high weight loss is a direct cause of adult mortality and whether, by withholding food, parents actually retain more for themselves.

The growth rate of chicks in two-chick broods is negatively related to the feeding latencies of their parents (unpublished data). Offspring of younger parents have a lower growth rate compared to that of older parents (Pugesek 1983), thereby, increasing the amount of time chicks are vulnerable to predation and cannibalism (Kennedy 1973; Hunt and McLoon 1975).

An alternative hypothesis to parental effort explaining age-related differences in food withholding behavior is that younger gulls are less experienced parents. Therefore, they are unable to respond properly to begging by chicks and are unable to locate sufficient amounts of food. Parental experience can be divided into two components; one in which previous experience produces learning or physiological changes that cause parents to modify behavior as they age and another component in which individuals become more efficient with age (Pugesek 1983). If learning or physiological change caused older parents to withhold food less frequently but reducted their potential to invest in future offspring, then the experience and effort hypotheses are not mutually exclusive. Age-related differences in foraging efficiency are not likely explanation of observed differences in feeding latencies (Pugesek 1981, 1983, 1984, 1990).

Both feeding latency and DPC support Triver's third prediction, indicating a longer period of parental care among older parents compared to younger parents. This conclusion assumes that a longer period of parental care reduces the ability of adults to invest in future offspring and increases the ability of offspring to survive and reproduce.

The negative relationship between adult survival and DPC indicates that the first assumption is valid. Parental age was used as a covariate in the analysis of survival and DPC to parcel out possible effects of declining survival with age. Mean DPC adjusted for the age covariate increased slightly among survivors and decreased slightly among nonsurvivors because older gulls had higher durations of parental care and died at a higher rate compared to younger gulls. However, controling such age-related variation had little effect on the strong relationship between survival and DPC. These results indicate that DPC is a valid measure of parental effort and that the reduced survival among older gulls observed here is due to higher levels of such effort.

The association between DPC and survival reported here should be interpreted cautiously. Results are nonexperimental and are, therefore, subject to the standard caveats for making causal interpretations between dependent and independent variables (Reznick 1985). It is likely that DPC covaried with a number of other behaviors that represented high levels of reproductive effort among parents. The combined effects of these behaviors resulted in differences in survival observed here.

The assumption that a longer period of parental care among older parents increases offspring survival and reproductive potential is supported by the observation that offspring of older parents receive feedings over a longer period of time and fledge at a greater size (Pugesek 1983). High offspring mortality rates shortly after offspring gain independence (Fordham 1968; Parsons and Duncan 1978; Threlfall 1978) suggest that energy reserves received from parents may be a critical determinant of survival. In addition, size at maturation may influence the ability to reproduce as adults. However, continued research is necessary to determine whether larger offspring also have greater future reproductive potential.

It seems remarkable that only a 5-day difference in DPC separates survivors and nonsurvivors in a reproductive cycle that takes upwards of 4 months to complete (Pugesek 1983). However, several other lines of evidence indicate that most reproductively induced mortality results from the cumulative results of the entire breeding season. First, there is apparently little mortality cost for gulls to migrate to the breeding grounds and lay eggs. Yearly survival rate of gulls whose nesting attempt terminates during the incubation phase of breeding is 92% compared to 72% among gulls that carry out the reproductive cycle (Pugesek and Diem 1990). Second, clutch size (Pugesek 1987) and number of chicks surviving 1 week posthatching (unpublished data) are poor predictors of adult survival. Number of offspring surviving 2 weeks posthatching (unpublished data) and fledging success (Pugesek 1987; Pugesek and Diem 1990) are increasingly strong predictors of adult survival. Finally, most of the adult mortality related to reproduction occurs after offspring are fledged (Pugesek 1987).

The last days of the parental care phase may be critical to adult survival in that some critical threshold may be reached beyond which it becomes difficult for gulls to return to prime physical condition. During the last days of the parental care phase, adults provide food for maintenance and growth to two chicks, each of which are the size of adults. It is likely that the energetic demands placed on adults accelerate rapidly near the time of fledging, and this is a time when adults are already in poor physical condition (Pugesek and Diem 1990). This is particularly true among older parents who, throughout the course of parental care, are less likely to withhold food from offspring compared to younger parents.

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References

Berger J (1979) Weaning conflict in desert and mountain bighorn sheep (*Ovis canadensis*): an ecological interpretation. Z Tierpsychol 50:188–200

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

Coulson JC, Monaghan P, Butterfield J, Duncan N, Thomas C, Shedden C (1983) Seasonal changes in the herring gull in Britain: weight, moult, and mortality. Ardea 71:235–244

Davies NB (1976) Parental care and the transition to independent feeding in the young spotted flycatcher (*Muscicapa striata*). Behaviour 59:280–293

Fordham RA (1968) Dispersion and dispersal of Dominican gulls in Wellington, New Zealand. Proc N Z Ecol Soc 15:40–50

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

Hunt GL Jr, McLoon SC (1975) Activity patterns of gull chicks in relation to feeding by parents: their potential significance for density-dependent mortality. Auk 92:523–527

Kennedy JR (1973) A study of the breeding colony of California gulls (*Larus californicus*), Bamforth Lake, Albany County, Wyoming. MS thesis, University of Wyoming, Laramie

Low BS (1978) Environmental uncertainty and the parental strategies of marsupials and placentals. Am Nat 112:197–213

Parsons F, Duncan N (1978) Recoveries and dispersal of herring gulls from the Isle of May. J Anim Ecol 47:993–1005

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 (1987) Age-specific survivorship in relation to clutch size and fledging success in California gulls. Behav Ecol Sociobiol 21:217–221

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

Pugesek BH, Diem KL (1990) The relationship between reproduction and survival in known-aged California gulls. Ecology 71:811–817

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

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

Stamps J, Clark A, Arrowood P, Kus B (1985) Parent-offspring conflict in budgerigars. Behavior 94:1–40

Threlfall W (1978) Dispersal of herring gulls from the Witless Bay Sea Bird Sanctuary, Newfoundland. Bird-Banding 49:116–124

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man, 1871–1971. Aldive, Chicago

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

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

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

Zeveloff SI, Boyce MS (1980) Parental investment and mating systems in mammals. Evolution 34:973–982