Parent-offspring cooperation in the blue-footed booby (Sula nebouxii): social roles in infanticidal brood reduction

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Summary. Reproduction in the blue-footed booby was examined for evidence of parent-offspring conflict over infanticidal reduction of the brood. Parental investment was analysed by measuring clutch characteristics, and chick growth and mortality in four seasons. Direct observations were made of behavioral development to determine the social roles of family members. The modal clutch was two similar-sized eggs, which hatched 4.0 days apart due to a 5.1-day laying interval and immediate incubation of the first egg. On average, senior chicks grew faster than their sibs in years of good or poor growth (Fig. 2), maintaining the initial size disparity for at least 65 days (Fig. 1). Differential mortality of junior chicks was associated not with poor personal growth, but with a 20–25% weight deficiency of the senior sib, implying siblicidal brood reduction triggered at a weight threshold. Senior chicks established behavioral dominance through low-frequency pecking, but ordinarily did not eliminate their sibs nor substantially suppress their begging (Fig. 3), even when their own growth was 16% below potential. Parents fed dominant chicks more frequently than subordinates, but did not intervene in inter-sib aggression, even when it reached a siblicidal level. The weight and possibly the dominance relation between sibs was inverted in 12% of pairs. The theoretical prediction of conflict over elimination of the junior chick was not supported; rather, parents and senior chick cooperate, as if their fitness interests were congruent. Further, provisional tolerance of the junior chick by its underweight senior sib is consistent with "self-sacrifice" to increase the latter's inclusive fitness.

Introduction

Current theory, based on assumptions regarding the inheritance of behavioral tendencies, predicts parent-offspring conflict in sexually-reproducing species over allocation of parental resources between sibs, with "selfish" offspring striving to distort investment in their own favor (Hamilton 1964; Trivers 1974; Macnair and Parker 1979; Parker and Macnair 1978, 1979; Stamps et al. 1978; Stamps and Metcalfe 1980; Parker 1985). Conflict is expected because each offspring is twice as related to itself as to its full sibs, whereas parents are equally related to each offspring. However, empirical support is weak and ambiguous, and the proposition that natural selection generates conflicting reproductive strategies in parents and offspring should be regarded as tentative.

O'Conner (1978a) extended the theory to the case of facultative avian brood reduction, an adaptive system whereby many bird species adjust their brood size to low food abundance by eliminating one or more of their progeny. This system has long been regarded as an adaptation for maximising parental reproductive success (Lack 1947, 1966; Ricklefs 1965; Russell 1972; Proctor 1975; Howe 1976; review in Mock 1984a), but current socio-biological thinking stimulates us to question which family members' interests it serves. Only in three (ardeid) infanticidal brood-reducers is the relevant social behavior well known (Mock 1984a, b; Fujioka 1986), but it appears that chick loss in many species is due to sib aggression (sibicidal), which parents do not attempt to thwart (see Young 1963 and Spellerberg 1971a for a possible exception).

O'Conner (1978a) showed that according to circumstances, the genetic interests of parents, surviving chick or even the victim chick can be advanced by this infanticide. Further, the food scarcity threshold for its occurrence is different for those parties. Specifically, in food-limited species with small broods, the senior chick is predicted to favor elimination of its sib before its parents do, resulting in inter-sib aggression and parental defence of the junior chick; that is, overt behavior-
al conflict between parents and senior chick. Recent theoretical explorations of parent-offspring conflict, taking into account evolutionary retaliation by parents (Parker and Macnair 1979; Parker 1985), have generated essentially the same prediction: we should see behavioral conflict.

To test these proposals, we looked for conflict in a species in which it is expected. The blue-footed booby (Sula nebouxii) is a colonial, ground-nesting marine bird that raises 1–3 chicks according to ecological conditions (Nelson 1966, 1978). Nestlings are fed by both parents, which regurgitate whole or predigested fish into the offsprings' mouths. When prey are scarce, the junior chick is reportedly sacrificed to promote its sib's survival. The aggressor is apparently the senior chick, which enjoys a competitive age/size advantage due to a substantial hatching interval (Nelson 1978). This bird, with its small brood, large size, exposed nest, and high tolerance of human proximity, is ideal for scrutinizing behavioral interactions.

To determine the pattern of post-hatch parental investment between junior and senior sibs, we compared the growth and mortality of nestlings in four reproductive seasons. A common assumption of the facultative brood reduction hypothesis is that the senior chick, acting selfishly to ensure its own survival, eats all it needs, while its sibling takes what, if anything, is left (e.g. Ricklefs 1965; O'Connor 1978a; Ryden and Bengston 1980; Braun and Hunt 1983; Mock 1985). Other things being equal, this "left-overs" hypothesis implies that the mean growth rates of senior chicks in different years should be similar, whereas the growth of junior chicks should be poor in years of scarcity and equal to that of their sibs in years of abundance. By comparing several seasons with, hopefully, natural interannual variation in food availability, it should be possible to detect that pattern, or such possible alternatives as equal food distribution between chicks or distribution in some fixed proportion. Initial investment in brood members was described by measuring clutch size, egg size, and laying and hatching intervals. To describe the social behavior mediating food distribution and chick loss, intensive longitudinal observations were made on several families with twin nestlings.

Methods

Initial investment, growth and mortality

Permanent quadrats were established over 15,000 m² of the blue-foot colony on Isla Isabel, Nayarit, off the Pacific coast of Mexico (21° 52'N, 105° 54'W) in 1982. A numbered peg was set by every nest and nest contents were recorded every three days in 1982 and 1984, and every four days in 1983, throughout the 3–4 months of the main nesting periods. In 1981 temporary quadrats within the same area were used, with nest contents recorded every two days. Eggs were marked according to observed laying order with spots of paint. Chicks were initially labelled with a colored leg band according to their hatching order, and on becoming mobile were assigned individual codes by using three bands.

In 1981 freshly laid eggs were weighed on an Ohaus triple-beam balance and measured with a Vernier. Clutch size was calculated in that year, using only nests where all laying occurred during the period of study. Chicks were weighed each year on every nest-check (every other nest-check in 1981) with Pesola spring balances of 300 g and 2000 g, whose negligible inter-annual variation was confirmed with an electronic balance. Chicks were deemed to hatch midway between the day first encountered and the previous nest-check. Death was recorded when a chick disappeared or its cadaver was found.

In 1983, the El Niño southern oscillation drastically increased chick mortality, so that very few chicks survived at all. Consequently, insufficient data are available for analysing growth in that year.

Behavior

Behavioral roles of parents and chicks were determined in 1982 by observing seven two-chick nests continuously during all daylight hours on every third day, from shortly after hatching of the junior chick until it was 60 days old. Five additional nests were observed during the same hours every second day for roughly 2 weeks in 1981. Observers sat unobtrusively several meters away, two of them alternating in 2-h shifts from 0600–1800 hours. Paint spots on the chicks' heads facilitated identification, and several hours of interobserver reliability training and periodic testing ensured consistent criteria for strictly-defined behavioral categories.

The absolute frequencies of feeds and inter-sib pecks were recorded, as well as the presence or absence of begging in every 2-min interval. It was sometimes difficult to decide whether any food was actually transferred, so a feed was scored whenever a small chick lodged its head in its parent's mouth or whenever a large chick hooked up its bill completely to that of its parent (feeding and agonistic behavior are described in Nelson 1978).

Development was analysed by dividing time into 10-day blocks, starting from each chick's estimated hatch-date, and mean daily behavioral frequencies were calculated for each chick in each block, making possible a true age-for-age comparison of sibs. Since observations of senior chicks were not made until their sibs hatched, the first block for both chicks used only data from age 5–10 days. Feeds were analysed by absolute frequency and by bout frequency. Using the interval frequency histogram method (Lehner 1976), we found that feeds within 10 min of each other were grouped in the same bout. If both chicks participated in the same bout, each was scored one bout.

Results

Initial investment, growth and mortality

In 1981, 36% of females laid a single egg, 58% 2 eggs and 6% 3 eggs (n=174). Mean weight of first eggs was 57.3 g (SD=6.9, n=120), second eggs 57.1 g (SD=4.9, n=86). Mean length and breadth of first eggs were 61.0 × 41.0 mm (SD=...