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Contributions of marginal offspring to reproductive success of Nazca booby (*Sula granti*) parents: tests of multiple hypotheses

Abstract While obligate siblicide is a phylogenetically widespread behavior, known from plants, insects, birds, and other taxa, with important implications for life history evolution, comprehensive evaluations of its costs and benefits to parents are rare. We used 12 years of breeding and band resight data to evaluate the importance of several potential benefits that marginal offspring (the usual victims of obligate siblicide) could provide to parent Nazca boobies (*Sula granti*), a seabird. We found no evidence for the resource-tracking hypothesis: 99.95% of two-chick broods were reduced to one chick before fledging, and the single exceptional brood probably lost one chick between fledging and independence. Behavioral observations indicated that siblicidal aggression caused most mortality of marginal chicks, and at least contributed to the remainder. We also found no evidence that marginal offspring provide a food resource for other family members. Marginal chicks benefit parents via adoption into other families, and possibly also in the context of progeny choice, but these benefits are minor compared to the insurance that marginal chicks provide against early failure of core (first-hatched) offspring. Further evaluation of the Insurance Egg Hypothesis showed that marginal and core offspring are functionally equivalent in the absence of sibling interactions, and that core offspring incur no detectable costs from behaving siblicidally. Nazca boobies are truly obligate brood reducers, with parents receiving principally insurance benefits from marginal offspring, but many birds and other taxa exhibiting persistent, unconditional sibling aggression do not exhibit universal brood reduction. Insurance is only one of several potential benefits that marginal offspring can confer on parents, and a multi-hypothesis approach to decompose the different types of benefits is required to understand the evolution of clutch size in other obligately siblicidal species.

Keywords Insurance egg · Resource tracking · Progeny choice · Adoption · Sibling competition

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Analysis of clutch size variation has strongly influenced the empirical study of life history evolution, with David Lack's seminal papers on birds guiding much of the progress. Lack understood the optimal clutch size in terms of the parents' capacity to deliver food to dependent offspring (Lack 1947). Since food supply may vary unpredictably, parents may link a large clutch appropriate for a food-rich year with resource tracking, mediated by staggered hatching and sibling competition, to bring food demand into line with supply in food-poor years (known as "brood reduction" or "resource tracking"; Lack 1947; Ricklefs 1965; Temme and Charnov 1987). Fine-tuning of Lack's basic idea incorporated costs of reproduction paid by parents that lower the optimal clutch size in iteroparous animals (Stearns 1992). This paradigm based on food-limited brood size, and secondarily on temporal variation in the degree of food limitation, motivated an extensive literature regarding the ability of resource tracking to explain laying patterns in birds.

Mock and Forbes (1995) introduced the terms "core offspring" and "marginal offspring" to differentiate the subset of the eggs or the young that parents can typically support (core offspring) from those that often appear to be

extra. Operationally, marginal offspring are recognized by their later positions in hatching sequences, and they bear corresponding age, size, and developmental handicaps (Krebs 1999). The number of core offspring indeed seems to be closely related to the parents' ability to provide food, as Lack proposed, but variation in the number of marginal offspring remains problematic. Some bird species lack marginal offspring altogether, such as single-egg eagles and seabirds. For species with marginal offspring, Lack's resource tracking is only one of their several potential benefits, including identifying defective core offspring through competition, replacing accidental failures of core offspring, and providing living food storage units. As Mock and Parker (1997, p 6) noted, parents producing marginal offspring "may be better prepared for environmental stochasticity (the "good year"), ready for accidents involving the core brood, and also alert to the possibilities of weeding out an ontogenetic disappointment and judiciously upgrading that slot. If none of these events arise, the extra kid can be lunch for somebody." The possibility of stealing parental care can be added to this list, if other families can be induced to adopt marginal offspring and raise them. At least 150 bird species exhibit adoption of young from outside the family (Riedman 1982); often such adoptions appear to be low-frequency mistakes made by parents using otherwise effective mechanisms to protect and provision legitimate offspring (Holley 1981; Williams 1994).

Marginal offspring in obligately siblicidal species are portrayed as offering little or no fitness benefit of the first type (Lack's resource tracking), because core offspring show unconditional, persistent aggression toward their marginal sibling(s) (e.g., Gargett 1978), and generally kill them whether food is abundant or scarce. Explanations for the existence of marginal offspring in such species have focused on the insurance value conferred by marginal offspring (reviewed by Anderson 1990; Mock and Parker 1997). However, many bird species meeting the typical criterion for obligate brood reduction (≥90% mortality of marginal chicks due to bullying by the core; Simmons 1988; Anderson 1990) fledge more than one chick on occasion (Steyn 1973; Cash and Evans 1986; Tershy et al. 2000; Osorno and Drummond 2003), so parents have more than one incentive (Forbes and Mock 2000) to produce marginal offspring. Mock and others have urged a pluralistic view of the existence of marginal offspring, in counterpoint to the historical focus on resource tracking in most birds, and on the insurance benefit in obligately siblicidal birds (Mock and Forbes 1995; Mock and Parker 1997; Forbes and Mock 2000). The skepticism of some authors regarding the insurance value of marginal offspring in birds (Lack 1966; Nelson 1966; Mead and Morton 1985; Lessells and Avery 1989; Bollinger et al. 1990; Simmons 1988), and their emphasis on alternative benefits (especially resource tracking in hypothetical rare years of high resource abundance) provide further motivation for the multi-hypothesis approach, even for obligately siblicidal species.

Obligately siblicidal Nazca boobies (*Sula granti*; Pitman and Jehl 1998; AOU 2000; Friesen et al. 2002) provide experimental evidence of the insurance fitness benefit, in which the second egg in two-egg clutches often produces a viable chick when the core egg fails or the core chick dies before it kills its sibling (Clifford and Anderson 2001a). When both eggs hatch, the second chick typically hatches 5–6 days after the first at a considerable physical disadvantage, and brood size is usually reduced to one chick shortly after hatching by sibling aggression (ejection from the nest scrape; Anderson 1989a). Here, we expand our evaluation of this Insurance Egg Hypothesis (Dorward 1962), testing the idea that marginal offspring are propagules of equivalent fitness to core offspring, and are not permanently handicapped by their marginal status. In a complementary manner, we test the hypothesis that siblicidal offspring incur no extra costs compared to nonsiblicidal core offspring, both in the near term (as a nestling) and the long term (until adulthood). Both hypotheses predict that survival, developmental rate, asymptotic body size, and survival to adulthood will not differ between groups. Few studies have evaluated the relationship between the place in a brood's competitive hierarchy and post-fledging performance. Some have found little effect of nestling competitive status, or core/marginal status, on juvenile or subadult survival/performance, or on breeding success (Evans 1997; Velando 2000; Roulin 2002; Drummond et al. 2003; Brown and Roth 2004), but interpretation of this result may be confounded by incomplete natal philopatry leading to differential dispersal based on nestling experience. Other studies did detect poor adult performance by marginal offspring (Spear and Nur 1994; Thomas et al. 1999), or reduced post-fledging survival (Husby 1986; Spear and Nur 1994; Slagsvold et al. 1995), but again incomplete philopatry could introduce bias. To determine whether any of these effects introduce costs relevant to selection on production of marginal offspring, we use a long-term database to compare the pre- and post-fledging survival of marginal offspring vs. core offspring, and of siblicidal core chicks vs. core chicks lacking a sibling. Natal philopatry and adult nest site fidelity are extremely high in this species (Huyvaert and Anderson 2004), minimizing the potential problem of differential dispersal. Extra-pair fertilization appears to be absent in the study population (Anderson and Boag, unpublished data; Anderson et al., unpublished data), removing a potentially confounding factor regarding the value of offspring to fathers.

To provide a multi-hypothesis approach to the existence of marginal offspring (Mock and Forbes 1995), we tested the following additional hypotheses regarding the fitness benefits that they could confer.

Resource-Tracking Benefit, assuming that both core and marginal offspring occasionally survive over the 9 years of the study, and predicting a reproductive advantage of parents with marginal offspring over parents without marginal offspring, in years of high resource abundance.

Icebox Benefit (Ingram 1959; Alexander 1974), assuming that marginal offspring represent a fresh store of food to the rest of the family in a predatory species, and predicting that consumption of marginal offspring during food shortages confers a reproductive advantage on parents with marginal offspring over parents without marginal offspring. Within-family cannibalism is known from a number of predatory bird species (Bortolotti et al. 1991; Stanback and Koenig 1992; Reynolds 1999). Nazca boobies are predators of fish and squid (Nelson 1978; Anderson 1989b) and their sister taxon, the masked booby (*Sula dactylatra*; Pitman and Jehl 1998; Friesen and Anderson 1996; Friesen et al. 2002), is known to eat similarly sized chicks of sooty terns (*Sterna fuscata*; M.C. Hazin, personal communication).

Adoption Benefit (Holley 1981), assuming that offspring are sometimes accidentally adopted by other families, and predicting that parents producing marginal offspring have a higher probability of producing a low-cost offspring through adoption than do parents producing only core offspring. In the case of Nazca boobies (a ground-nesting species), core chicks expel marginal chicks from the nest, and adoption is the only viable option of marginal chicks after expulsion. In addition, foreign eggs may be adopted if displaced downhill into the vicinity of another nest (Clifford and Anderson 2001a; Humphries and Anderson, submitted).

Progeny Choice Benefit (Kozlowski and Stearns 1989), assuming competition between marginal and core chicks would reveal deficiencies in the core chick, and predicting that sometimes the core chick *loses* in competition to the marginal chick.

Methods

Demographic data collection

We conducted this research at Punta Cevallos, Isla Española, Galápagos Islands (1°20′S, 89°40′W), the site of our long-term studies of booby breeding biology [Anderson and Ricklefs (1987), and Huyvaert and Anderson (2004) give details of the study site]. During the breeding seasons of 1985–1986 and 1992–1993 through 2000–2001, we or our assistants collected daily nest histories from 285 to 1,296 nests each year, determining the clutch size, the number of eggs hatched, and survivorship of nestlings in each nest. First-laid eggs were marked with an "A," and second laid-eggs with a "B." In 2001–2002, we also wrote the nest number on each egg. During the breeding seasons of 1983–1984 and 1984–1985, we collected daily nest histories at 193 and 205 nests, respectively, through approximately the first half of the nestling period, providing data on hatching patterns but not on overall breeding success. To identify the types of benefit that parents receive from producing marginal offspring, we focus on the 2,799 families in which at least one egg of a two-egg clutch hatched.

From 1992 to 1993 on, monitoring of each nest was continued at least until most chicks reached a developmental stage at which pennaceous juvenile plumage had replaced all but 1% of the downy chick plumage. We refer to this developmental stage as the "1% down" stage (mean age = 100.9 days, SD = 8.8), and we measured mass, culmen length, ulna length, and flattened wing chord on that day, and banded them on or before that day. Chicks accumulated guano on their feet after hatching, which washed off during their first flight to the sea. We considered a chick fledged on the first day that its feet were clean. Offspring leave the colony for at least 2 years on average 44.7 days (SD = 9.80; unpublished data) after fledging. During this period after fledging and before departing the colony, fledglings continue their attachment to the nest site at night and to receive parental care, but they are frequently away from the colony during daylight nest monitoring. During the 2001–2002 breeding season, all offspring were monitored by both day and night checks until the date that they disappeared from the colony to validate the use of the 1% down developmental criterion as a proxy for reaching independence from parents; in other years we discontinued systematic monitoring after the 1% date. Age at 1% down in 2001–2002 was strongly correlated with both age at fledging (Spearman $r = 0.69$, $df = 55$, $P < 0.001$) and age of leaving the colony ($r = 0.48$, $df = 51$, $P < 0.001$). For chicks with known ages of 1% down and of fledging, fledging occurred on average 15 days (SD = 16.11) after a chick reached the 1% stage; this figure omits 1/267 (0.37%) of the chicks reaching 1% down, because the chick died before fledging. Five of the 266 fledglings (1.88%) were observed dead after fledging. These low mortality rates were consistent with those of other years with less complete data, and we assumed that chicks reaching the 1% stage also reached the age of independence. We assessed chick status at the 1% down stage rather than at fledging for several reasons: fledglings may be dependent on parental care but not present on land during daylight monitoring; they are more difficult to catch; the ages at which the two stages are reached are highly correlated; growth is essentially complete at the 1% down stage; and little mortality occurs after the 1% down stage.

Recruitment of offspring into the adult population was assessed through annual band resight surveys during the incubation period (see Huyvaert and Anderson 2004 for complete details of the method). Mark-capture modeling indicated that > 99% of birds present at that time were recaptured (Huyvaert and Anderson 2004).

Behavioral data collection

During the 2002–2003 breeding season, we observed 29 two-chick broods continuously when ambient light permitted (0510–1850 h) from a distance of 4–10 m, recording all nestling begging, aggression, feeding,

distress calls, ejections from the nest scrape, and parental interventions in sibling aggression on a palm computer; most of these results will be reported elsewhere. When one of the two nestlings died, we ended the nest watch. If one nestling was ejected, we ended the nest watch but continued watching the ejected chick during daylight hours to determine the ultimate cause of death, or whether adoption occurred. The spatial distribution of two-chick broods, the timing of their hatching, and the number of observers limited observation to a single nest at one time. Brood reduction occurred within 10 days of the marginal chick's hatching in all nests except one; we ended continuous observation of this nest after 6 days, but continued checking it several times each day to determine the fates of the two chicks.

Statistical methods

To compare probabilities of surviving to the 1% down stage for chicks of different types (see Table 1), we used the Generalized Linear Models module of Statistica (StatSoft Inc. 1999) to construct a categorical logistic regression (a binomial distribution with a logit link function). We used all years with adequate samples of fledglings (1992–1993, 1993–1994, 1994–1995, 1995–1996, 1996–1997, and 2000–2001); the excluded years were cases of high breeding failure (unpublished data). The model generates W, the Wald Statistic, for comparison to the chi-square distribution for tests of significance. We used adjusted hatching date as the covariate, and chick type (core with no marginal vs. marginal with no core, and core with marginal vs. core without marginal) as a categorical variable. Adjusted hatch date is the actual hatch date minus the mean hatch date for that year; we made this adjustment because hatch dates differed among years (two-way ANOVA, year effect: $F_{5,488} = 26.35$, $P < 10^{-6}$; chick type effect: $F_{1,488} = 0.004$, $P = 0.95$; year × chick type interaction: $F_{5,488} = 1.46$, $P = 0.20$). As a result, hatch dates showed only partial overlap across years, but adjusted hatch dates showed essentially complete overlap. We used the

Table 1 Outcome in two-egg clutches in which at least one hatched, all years combined. In one two-chick brood, the marginal reached the 1% down stage, but in very poor condition, and appeared likely to die. The value for Type 6 assumes that this marginal chick died between the 1% down stage and independence

Type	Nest history	Frequency
1	Core hatched, marginal hatched, marginal died	1,877
2	Core hatched, core died, marginal hatched	72
3	Core hatched, marginal hatched, core died	24
4	Core hatched, marginal failed	596
5	Core failed, marginal hatched	230
6	Core hatched, marginal hatched, both survived	0

same logistic regression technique to compare probabilities of returning to the colony as an adult. Offspring return to the Punta Cevallos colony at ages 2–13 years as adults; 98% return by age 8 years (Huyvaert 1999). To allow fledglings 8 years to return at least once as adults, we only used the 1993–1994 and 1994–1995 cohorts (the 1992–1993 season produced no adults that had been a core chick with an unhatched sibling, precluding analysis of that year).

To compare body sizes of core and marginal chicks, both lacking siblings (Types 4 and 5 in Table 1; see below), we used the General Linear Models module of Statistica to perform a MANCOVA with year and chick type as categorical variables, four size parameters as dependent variables, and adjusted hatch date as the covariate. The assumption of equal slopes was satisfied for both the year comparison (Wilk's Lambda = 0.92, Rao's $R_{25,930} = 0.87$, $P = 0.64$) and the chick status comparison (Wilk's Lambda = 0.99, Rao's $R_{5,254} = 0.60$, $P = 0.70$). We used a nonparametric comparison of age at which the chick reached the 1% down stage because this variable did not meet the assumption of homogeneity of variance; all the size parameters did meet this assumption.

To compare body sizes of core chicks with and without a sibling (Types 1 and 4 in Table 1), we used a separate slopes model within the General Linear Models module of Statistica, because the parallelism assumption was not satisfied for the year comparison. As above, we used a nonparametric comparison of age at which the chick reached the 1% down stage, because this variable did not meet the assumption of homogeneity of variance. Evaluations of body size used all years with adequate samples of measured chicks (1993–1994, 1994–1995, 1995–1996, 1996–1997, and 2000–2001).

To evaluate the equivalence of core and marginal offspring, we used only core chicks whose sibling egg did not hatch, and marginal chicks whose sibling egg did not hatch (Types 4 and 5, respectively, in Table 1). This comparison avoids any influence of sibling interactions on performance of surviving chicks whose sibling hatched (Types 1, 3, and 6). It also avoids the possibility that broods containing Types 2 and 3 chicks received unusually poor parental care, as is suggested by the early death of these chicks' core siblings.

Results

Insurance benefit and equivalence of core and marginal offspring

Six distinct nest histories were documented during this study (Table 1); three involved failure of the first offspring and so the possibility of an insurance benefit. The marginal offspring hatched and survived for at least 1 day after failure of the core offspring in 326 of the 2,799 (0.116) two-egg clutches. The most common form of insurance was replacement of an unhatched core egg

(230/326 = 0.706); the survival rate of these Type 5 (Table 1) marginal chicks to the 1% down stage was 0.542, demonstrating their ability to provide hatching insurance.

Marginal chicks with an unhatched core sibling survived to the 1% down stage as often as did core chicks with an unhatched marginal sibling [Fig. 1; logistic regression, hatch date effect: $W = 17.54$, $df = 1$, $P < 10^{-4}$; year effect: $W = 33.16$, $df = 5$, $P < 10^{-5}$; chick type (core vs. marginal): $W = 0.20$, $df = 1$, $P = 0.65$; year × type interaction: $W = 4.16$, $df = 5$, $P = 0.53$]. The body sizes at fledging of these marginal and core chicks did not differ either (Fig. 2; MANCOVA, year effect: Wilk's Lambda = 0.44, Rao's $R_{25,948} = 9.35$, $P < 10^{-6}$; chick type effect: Wilk's Lambda = 0.99, Rao's $R_{5,255} = 0.48$, $P = 0.79$; year × status interaction: Wilk's Lambda = 0.94, Rao's $R_{25,948} = 0.63$, $P = 0.92$). Marginal and core chicks with unhatched eggs did not differ in the age at which they reached the 1% down stage (Fig. 2; all within-year Mann–Whitney U-test $P > 0.29$), or in their probability of being sighted in the colony as adults (Fig. 3; logistic regression, hatch date effect: $W = 3.97$, $df = 1$, $P = 0.05$; year effect: $W = 0.57$, $df = 1$, $P = 0.45$; chick type effect: $W = 0.81$, $df = 1$, $P = 0.37$; year × type interaction: $W = 2.82$, $df = 1$, $P = 0.09$). Only four offspring from this

dataset have reproduced, precluding an analysis of breeding success.

Cost of competition

In terms of probability of survival to the 1% down stage, core chicks with a marginal sibling (Table 1, Type 1) did not differ from core chicks with an unhatched marginal sibling (Table 1, Type 4; logistic regression, adjusted hatch date effect: $W = 34.10$, $df = 1$, $P < 10^{-6}$; year effect: $W = 81.22$, $df = 5$, $P < 10^{-6}$; chick type effect: $W = 1.41$, $df = 1$, $P = 0.24$; year × type interaction: $W = 0.76$, $df = 5$, $P = 0.98$). Body size at the 1% down stage of these two types of core chick did not differ (Fig. 4; MANCOVA chick type effect: $W = 1.00$, $df = 4$, $P = 0.50$; year × chick type interaction: $W = 0.98$, $df = 16$, $P = 0.26$). In terms of the age at which chicks reached the 1% down stage, the two types of core chicks did not differ (Fig. 4; Mann–Whitney U-tests for each year, all P values > 0.05). They also did not differ in their probability of being sighted in the colony as adults (Fig. 5; logistic regression, hatch date effect: $W = 1.10$, $df = 1$, $P = 0.29$; year effect: $W = 1.44$, $df = 1$, $P = 0.23$; chick type: $W = 1.69$, $df = 1$, $P = 0.19$; year × chick type interaction: $W = 2.33$, $df = 1$,

Fig. 1 Logistic regressions of the probability of reaching the 1% down stage on Julian hatch date, separately for core chicks without a marginal sibling (Type 4, *straight line*), and marginal chicks without a core sibling (Type 5, *dashed line*) for 6 years of study, a 1992–1993, b 1993–1994, c 1994–1995, d 1995–1996, e 1996–1997, and f 2000–2001. Range of lines vary due to inter-annual differences in the hatch dates of surviving marginal and core chicks, and in investigator presence at the study site. Only one Type 4 chick reached the 1% down stage in 1992–1993
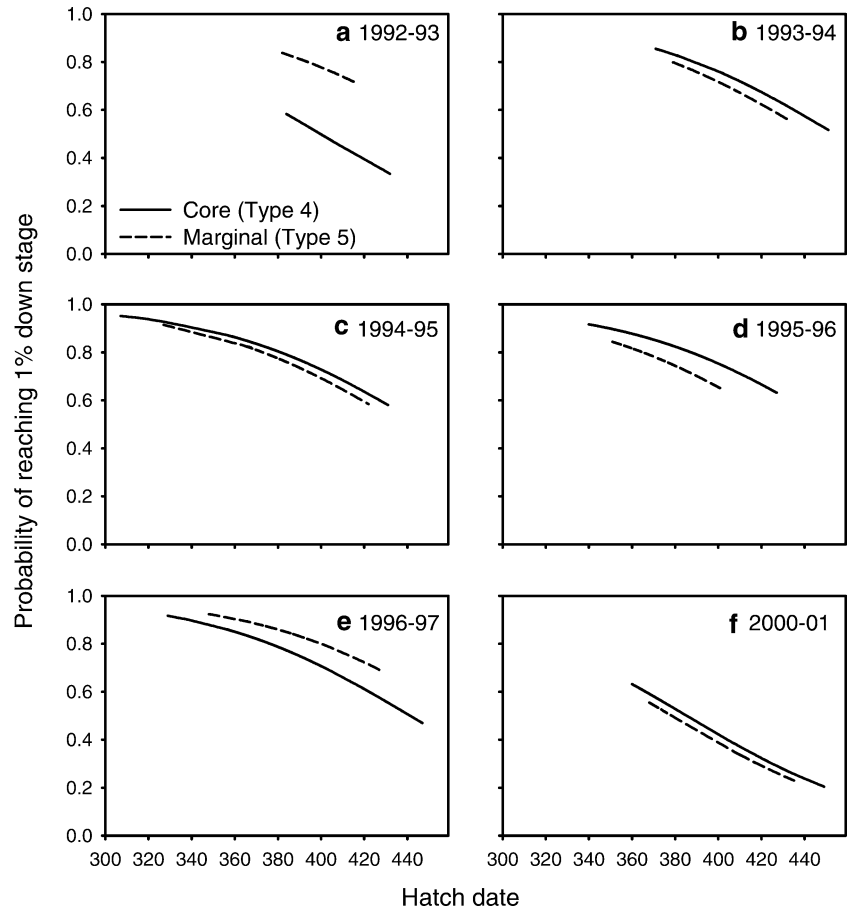
Fig. 2 Physical characteristics (mean and 95% C.I.) of core chicks without a marginal sibling (Type 4, *filled circle*), and marginal chicks without a core sibling (Type 5, *open circle*) at the 1% down stage: a mass, b wing chord, c ulna length, and d culmen length. e Median age (bracketed by 25th and 75th percentiles), age at which chick reached the 1% down stage. Sample sizes of each group are shown at the top
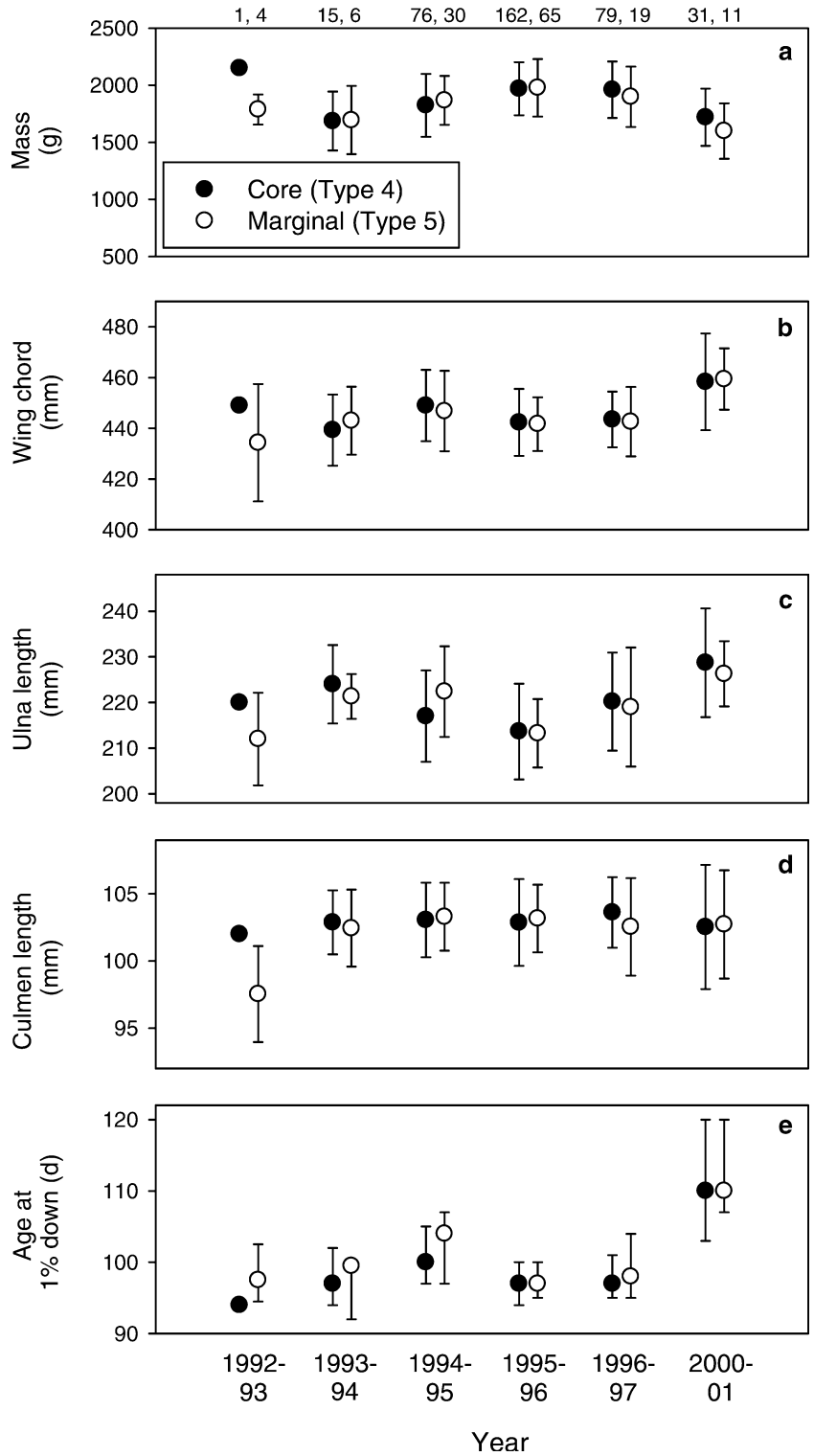
$P = 0.13$). Only four offspring from this dataset have reproduced, precluding an analysis of breeding success.

Resource-tracking benefit

Of the 2,799 two-egg clutches that produced at least one hatchling, 1,901 produced two-chick broods (in which two chicks were present together for some period of time) throughout the breeding season. Almost all of these broods were reduced to a single chick within 10 days of the second chick's hatching (Fig. 6). Several two-chick broods reached advanced ages before the death of one or both, but only one brood (in 1996–1997) maintained both chicks to the 1% down stage (Fig. 6). Compared to the mean values for 1996–1997, the smaller
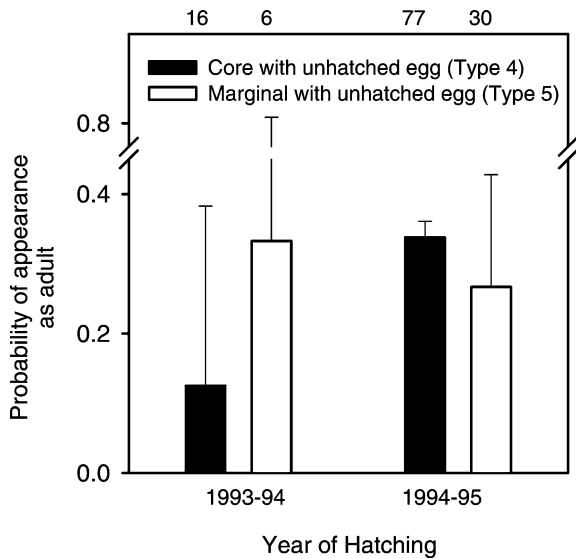
16   6   77   30

Fig. 3 Probabilities of appearance as an adult in the Punta Cevallos colony for two groups of chicks with unhatched sibling eggs: core chicks (Type 4, *black bars*) and marginal chicks (Type 5, *white bars*). Error bars are binomial 95% confidence intervals. Sample sizes of each group are shown at the top

chick in this brood was weak when measured at the 1% down stage, when its mass was 2.54 standard deviations below the mean for that year, and reached the 1% down stage at an age 4.12 standard deviations older than the mean age for that year. This chick almost certainly died before becoming independent, or shortly thereafter. Of the remaining two-chick broods followed to the 1% down stage, 557 (0.293 of these two-chick broods) lost both chicks, and 1,343 (0.706) broods had a single chick at the 1% down stage. The resource-tracking benefit (production of a 1% down stage chick) could accrue to parents from no more than one of the 2,799 (0.0004) two-egg clutches that hatched 1 + egg, no more than one of the 1,901 (0.0005) two-chick broods, and no more than one of the 1,344 (0.0007) two-chick broods producing 1% chicks. In fact, probably none of these families produced two independent offspring.

Icebox benefit

In each of the 29 two-chick broods under constant daylight observation, one chick died by the marginal chick's 21st day (median = 2 days, range 0–21 days); one of these deaths was of a core chick due to inability to feed properly. In 25 of the remaining 28 nests, the core chick ejected the marginal chick from under the brooding parent at least once during daylight hours, but the marginal chick was sometimes able to return. No marginal chick ever ejected a core chick. The total number of ejections during daylight prior to the marginal chick's death ranged from 0 to 22 (median = 4). In three cases, the marginal chick died within the nest scrape of hypothermia, starvation, and crushing by the parent,
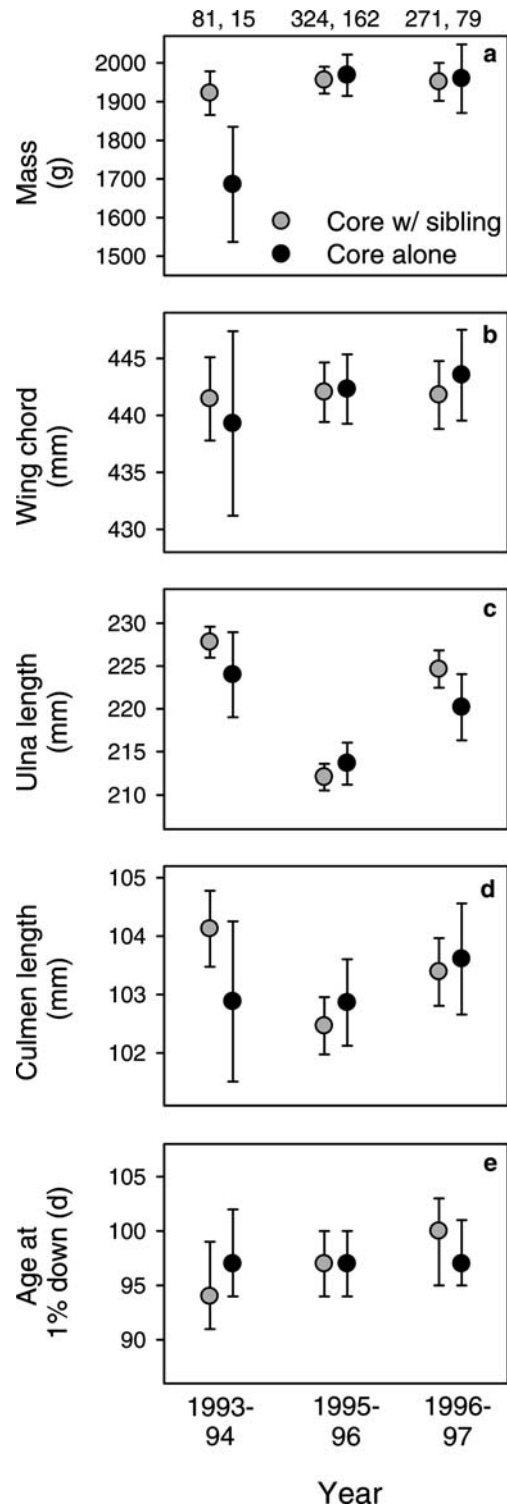
81, 15   324, 162   271, 79

Fig. 4 Physical characteristics (mean and 95% C.I.) of core chicks that had a sibling (Type 1, *open circle*), and those that never had a sibling (Type 4, *filled circle*) at the 1% down stage: a mass, b wing chord, c ulna length, and d culmen length. e Median age (bracketed by 25th and 75th percentiles), age at which chick reached the 1% down stage. Sample sizes of each group are shown at the top

respectively, and was not eaten by either parent or by the core chick before it was eventually ground into the nest substrate. In 23 cases of siblicidal ejection, the dead
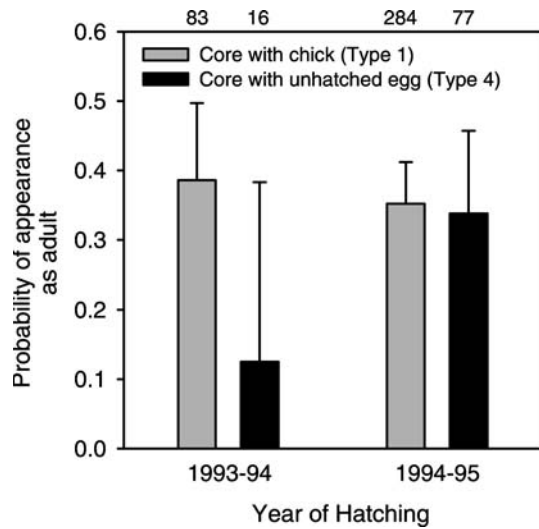
Fig. 5 Probabilities of appearance as an adult in the Punta Cevallos colony for two groups of core chicks: with a hatched marginal sibling (Type 1, *gray bars*), and with an unhatched egg (Type 4, *black bars*). Error bars are binomial 95% confidence intervals. Sample sizes of each group are shown at the top
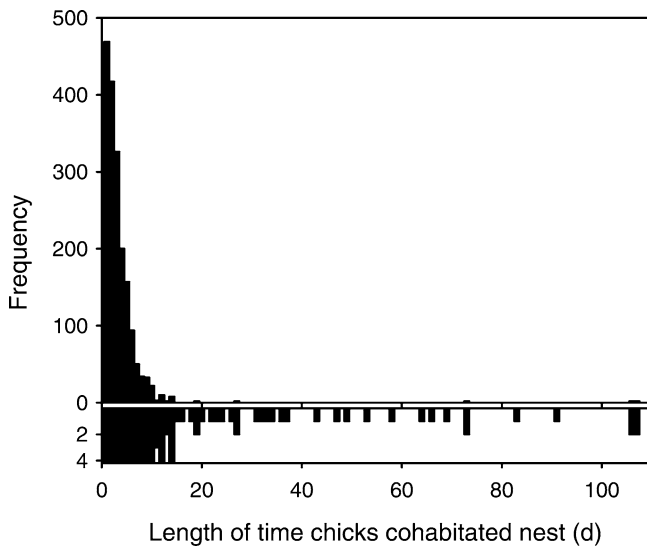

Fig. 6 Frequency distribution for two-chick broods of duration that chicks cohabited nest (upper panel). Lower panel adjusts vertical scale to enhance visibility of rare events in right tail of distribution

chick died away from the nest and was not eaten by family members, and instead was predated or scavenged by frigatebirds (*Fregata minor* and/or *Fregata magnificens*; seven cases), Sally Lightfoot crabs (*Grapsus grapsus*; six cases), Darwin's finches (*Geospiza conirostris*; one case), or an adult Nazca booby in a neighboring nest (one case); starved in a concealed place that precluded scavenging (three cases); killed by pecking from a neighboring Nazca booby adult (one case); or disappeared during the night (four cases, probably crab predation). In the remaining three cases, the marginal chick disappeared from the nest during the night; these three chicks could have been consumed by a family member, but we have no evidence that this occurred. The unprecedented case of a neighboring adult swallowing a wandering ejectee showed that cannibalism of nestlings does occur, but the icebox benefit could accrue to no more than three of the 29 broods (0.103). However, our observations at this site over the past 20 years lead us to suspect strongly that marginal chicks are never eaten by family members. All-day behavioral observations of a subcolony including (70 nests, throughout their incubation periods in two different years, revealed no consumption of either eggs or chicks by conspecifics (unpublished data). Furthermore, in approximately 15.7 person-years that we or our colleagues have spent working in the Punta Cevallos colony during hatchling periods since 1984, we have witnessed hundreds of sibling ejections, but no consumption of hatchlings by their own parent or by any other Nazca booby adult. Nazca booby siblings are similar enough in size to preclude sibling cannibalism due to gape limitation (personal observation).

Adoption

In the 2001–2002 season, in which every monitored egg was marked with its native nest number, 29 monitored eggs were adopted in another monitored nest (in addition, 13 unmonitored offspring were adopted by monitored families). Of the 29 monitored offspring becoming adoptees, 15 were from nests that originally had two-egg clutches. Of these 15, seven were marginal eggs and none were marginal chicks. None of these 29 adoptees reached the 1% down stage (but one of the 13 adoptees from an unmonitored nest did reach the 1% down stage in a monitored nest). The 2001–2002 estimate of the frequency of adoption represents our best estimate of this benefit: 29 offspring from 1,460 (0.0199) monitored nests were accepted into a different nest, and the adoption benefit could have accrued to parents of seven marginal offspring from 755 (0.009) two-egg clutches. In fact, none of the seven reached the 1% down stage. Alternatively, core offspring could be exported and marginal offspring retained; of eight adopted core offspring (six eggs and two chicks), none reached the 1% down stage.

Of 8,729 monitored nests providing less specific data between 1983–1984 and 2000–2001, we noted 77 additional confirmed adoptions. In at least one of these cases, both the remaining resident offspring and the adopted offspring fledged. In 39 of these adoptions, from two-egg clutches, we knew whether the core or the marginal egg produced the adoptee. Of these 39 events, 25 were adoptions of eggs and 14 were adoptions of chicks. Eighteen of the adoptees were core eggs (13) or chicks (5), and 21 were marginal eggs (12) or chicks (9). Ten adoptees reached the 1% down stage; five of these adoptees were core eggs (2) or chicks (3), and five were

marginal chicks. Thus, this larger sample indicates that the adoption benefit was received by parents of at least five of the 2,799 (0.0018) two-egg clutches with 1+ hatchling.

Progeny choice

Progeny choice requires two or more offspring to cohabit the nest and compete for the single permanent slot. The benefit of progeny choice can be accrued only when marginal offspring survive after the death of core offspring; simple replacement of a core offspring that would die in any case is an insurance benefit, not a progeny choice benefit. In the 1,901 broods with two contemporaneous chicks, 24 (0.013) marginal chicks survived for some time, after the death of their core sibling. These broods *might* have represented instances of a progeny choice benefit. The core chick died within 2 days of the marginal chick's hatching in 13 of the 24 (0.54) broods; Nazca booby hatchlings are highly altricial, and so feeble shortly after hatching that we consider it improbable that these marginal chicks contributed to the core chicks' deaths. The causes of death of these core chicks included trampling by the parents and choking on food, apparently unrelated to the marginal chick's presence. Of the remaining 11 broods, one pair of siblings died within 1 day of each other (likely from the same unknown causes and unrelated to sibling competition), and ten others cannot be rejected as cases of progeny choice. In only one case does direct evidence implicate the marginal chick in the core chick's death: in that case, the marginal chick evicted its sibling at age 23 days. Thus, 10/1,901 (0.005) two-chick broods could represent examples of marginal chicks outcompeting core chicks; of these, seven actually produced a chick at the 1% down stage. A strong case for the progeny choice mechanism can be made for only one of the 1,901 (0.0005) two-chick broods, and for only one of the 2,799 (0.0004) two-egg clutches with 1+ hatchling.

Discussion

Among birds exhibiting competition between siblings, Nazca boobies represent the epitome of intolerance. Other species with persistent, unconditional sibling aggression occasionally have surviving broods of two (Brown et al. 1977; Evans 1996; Tershy et al. 2000), but broods of two Nazca booby chicks were quickly reduced to a single chick in virtually all of the families that we studied. In only one family did two siblings survive to the 1% down developmental stage, and in this case, one of the chicks was in such poor condition that it almost certainly did not survive to independence. Given that caveat, Nazca boobies have truly obligate brood reduction, and our behavioral data indicate that sibling aggression accounts for most of the deaths of marginal chicks, and at least contributes to some extent to the remainder.

While obligate siblicide is a phylogenetically widespread phenomenon known from plants (Ganeshaiah and Uma Shaanker 1988), insects (Salt 1961; Rosenheim and Hongkham 1996), and other taxa (Mock and Parker 1997) in addition to birds, with important implications for life history evolution, comprehensive evaluations of its costs and benefits are rare. Our study appears to be the most complete of such an evaluation in several respects: the multi-year dataset encompasses significant environmental variety, including El Niño and La Niña years, and periods of both high and low reproductive success (Townsend 2004); the sample size is large; the predictions of several plausible hypotheses regarding benefits of marginal offspring were tested; and assumptions of the top hypothesis, involving insurance, were tested. Regarding the other hypotheses, Nazca booby parents occasionally received an adoption benefit by hatching two chicks and exporting one of them, but the magnitude of this benefit was small compared to the insurance benefit. Adoption-based selection for marginal offspring may be stronger than the infrequent benefit might suggest, however, because the genetic parents of the adoptee avoid most of the costly care of the offspring. A progeny choice benefit may have been realized very rarely, and an icebox benefit could not be ruled out, but appeared unlikely. In any case, the nutritive value of a cannibalized hatchling of 40–50 g is negligible compared to the daily food intake of adults (300–500 g; Anderson and Ricklefs 1992). We reject the resource-tracking hypothesis altogether. In contrast, the prediction of the Insurance Egg Hypothesis has been supported by both clutch size manipulations (Clifford and Anderson 2001a) and nonexperimental nest history data (Table 1), and the assumption that surviving marginal offspring eventually contribute to parental fitness was supported by data on marginal offspring's survival to adulthood.

Assessment of the obligate brood reduction of Nazca boobies reveals a remarkably effective set of adaptations to offset hatching failure, and secondarily the accidental death of the core chick. We found no evidence that marginal offspring were intrinsically inferior to core offspring (Figs. 1, 2, 3). Likewise, comparisons of core chicks with and without a sibling indicate that siblicidal interactions had no negative effect on survival and development, or survival to adulthood, of core offspring (Figs. 4, 5). The marginal offspring's equivalence to the core offspring does not prevent its rapid eviction by the core offspring when the insurance is superfluous, and the cancellation of the insurance policy imposes no detectable costs on core offspring due to their overwhelming phenotypic advantage derived from hatching asynchrony (Anderson 1989a), and the complicity of parents during the siblicide (Lougheed and Anderson 1999). Since the post-hatching replacement procedure appears to be cost-free, selection on clutch size (and so, on production of marginal offspring) is driven mainly by

the pre-hatching cost of egg production and the post-hatching benefit of insurance. We showed elsewhere that the cost of egg production appears to be similar in most members of the Sulidae (boobies and gannets), and that only species with poor hatching success produced marginal offspring, as expected under the Insurance Egg Hypothesis (Anderson 1990). Thus, the Insurance Egg Hypothesis provides a sufficient explanation for the production of marginal offspring in Nazca boobies, with adoption and progeny choice benefits making minor contributions to positive selection on parents producing a marginal offspring.

Given this selective influence on clutch size, the failure of approximately half of the breeders (the proportion varies with year) to produce second eggs (Anderson 1990) remains to be explained. Townsend and Anderson (in review) found no evidence that parents producing two-egg clutches incur a survival cost of reproduction that parents of one-egg clutches avoid, and only weak evidence of a fecundity cost. Nonetheless, Anderson (1990) used a cross-species study to deduce the existence of significant egg production costs in the Sulidae, and Clifford and Anderson (2001b) showed that supplemental feeding of females caused nearly all of them to produce second eggs. Hence, variation between females in proximate food limitation, and not in fitness tradeoffs at the ultimate level, seems to explain variation in clutch size. Two results implicate variation in overall parental quality in the clutch size variation: breeding pairs that produce two-egg clutches also are more likely to raise hatchlings to independence (Clifford and Anderson 2001a), and females tend to maintain their clutch size across years (Townsend and Anderson, in review). As a body, these results suggest that some Nazca booby females, or breeding pairs, consistently lack the foraging capacity during the egg formation period to produce second eggs, and to avail themselves of the benefits of marginal offspring.

Simultaneous measurement of the potential benefits of marginal offspring could bring clarity to the extensive and confusing literature regarding avian clutch size, hatching interval, and sibling competition. This field can be thought of as focusing on the cost–benefit tradeoff of producing marginal offspring, and the degree of handicap that marginal offspring are assigned by maternal effects such as asynchronous hatching. Clutch size and/or hatching interval are frequently manipulated, and reproductive output of the treatments is compared to test the resource-tracking hypothesis. Resource-tracking adaptations may in fact exist, but will be only weakly apparent if marginal offspring consistently provide other benefits in both good and bad food conditions. In that case, decomposition of the marginal offspring's benefits into those due to resource tracking, and those due to other effects, produce the specific data (distinct resource-tracking benefits) needed to test the resource-tracking hypothesis.

Mock and Parker (1986) provided a useful decomposition method, partitioning the contribution of marginal offspring into two fitness components: extra reproductive value (RV_e), obtained when both core and marginal offspring survive (or marginal offspring die but somehow facilitate the performance of core offspring, such as by providing themselves as a meal), and insurance reproductive value (RV_i), obtained when core offspring fail and marginal offspring, which are otherwise doomed, replace them (see also Lamey et al. 1996). RV_e is the contribution of marginal offspring under the resource-tracking hypothesis, yet RV_i provides a significant amount, or even most, of the benefit embodied by marginal offspring in many such partitions (Mock and Parker 1986; Mock et al. 1990; Evans 1996; Wiebe 1996). Other studies have detected a significant insurance benefit from last-hatched chicks without specifically calculating RV_i (Dorward 1962; Simmons 1967; Kepler 1969; Aparicio 1997; Tershy et al. 2000; Young and Millar 2003). The resource-tracking hypothesis assumes (in contemporary terms) that marginal offspring provide RV_e; if they do not, or if the contribution is minor compared to other benefits, then tests of the resource-tracking hypothesis are misguided. Ideally, the assumption that marginal offspring provide RV_e should be tested before experiments are conducted to test the resource-tracking hypothesis. In an excellent example of this kind of decomposition, Forbes et al. (2002) showed that marginal offspring of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) provide a mix of benefits: extra offspring via resource tracking in years of food abundance, an insurance benefit via replacement of core eggs that fail to hatch, and a progeny choice benefit via excess mortality of costly sons during food shortages. They also showed that the magnitude of these different contributions varies across years. Parents of some other species are also known to derive a mix of benefits from marginal offspring (reviewed by Wiebe 1996).

Finally, we draw attention to the possible conflation of the terms "obligate siblicide" and "obligate brood reduction." Obligately siblicidal behavior is unconditional (independent of food intake), persistent, and typically lethal aggression among siblings. In the case of Nazca boobies and some insects (Compere and Smith 1927; Flanders 1944), obligately siblicidal aggression leads to obligately (universal) brood reduction, but it may not do so in all obligately siblicidal species. For example, core chicks may attempt to kill marginal siblings, but be unsuccessful when resource availability is high. Simmons (1988) suggested that obligately siblicidal bird taxa that occasionally produce two fledglings [for example, 1/94 two-chick broods in American white pelicans *Pelecanus erythrorhynchos* (Evans 1996), 7/100 two-egg clutches in brown boobies *Sula leucogaster* (Tershy et al. 2000)] actually were tracking an unpredictable environment, and thus occasionally receiving the direct benefit (RV_e) envisioned by Lack. Parents in some obligately siblicidal species may well receive benefits from marginal offspring other than insurance against early failure of the core brood, and attention to the different

mechanisms by which marginal offspring impart reproductive value is required to quantify the importance of each mechanism.

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