

Production of insurance eggs in Nazca boobies: costs, benefits, and variable parental quality

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Numerous studies of birds have demonstrated the value of producing insurance eggs. We have previously found that second eggs provide insurance against failure of first eggs for Nazca boobies (*Sula granti*), which raise only one chick to fledging, yet some females lay only one egg. We used an 8-year data set to compare 2 hypotheses for clutch size variation: one based on trade-offs, predicting declining future performance by females that lay a costly second egg and one based on parental quality, predicting that intrinsically superior females lay 2 eggs both currently and in the future. Clutch size variation did not contribute to the best multistate mark–recapture model of survival, suggesting that clutch size and survival are unrelated and that any survival cost of reproduction related to laying second eggs is small. Transition probabilities between reproductive states were generally, but not entirely, inconsistent with fecundity costs of producing a marginal egg. Parental quality effects were apparent, with females tending to remain in a given reproductive state across seasons. Parents producing a marginal egg had consistently higher breeding success than did parents of 1-egg clutches, due principally to the insurance effect and secondarily to differences in parental quality after hatching. Different model selection approaches gave differing results for logistic regression analyses of breeding success of females that hatched eggs. A conventional significance-testing, iterative-fitting approach excluded insurance state from the top model, whereas the information-theoretic (I-T) approach detected an association between current insurance state and subsequent survival and fecundity. Using the I-T approach, potentially biological significant (but not statistically significant under conventional analysis) effects were detected that may otherwise have been ignored. *Key words:* clutch size, cost of reproduction, insurance hypothesis, model selection, multistate mark–recapture models, parental quality. [*Behav Ecol* 18:841–848 (2007)]

The concept of reproductive insurance was originally invoked to explain the production of second eggs in 2-egg clutches of bird species that seldom raise more than 1 of 2 offspring (Dorward 1962). In most of these species (including eagles, cranes, pelicans, and boobies; Anderson 1990), 2-chick broods are reduced to one by obligate siblicide: lethal, unconditional attacks by the older, stronger broodmate on its sibling. Mock and Forbes (1995) introduced the useful terms “core” and “marginal” offspring to differentiate young offspring that can typically be raised (core) from those that may have high mortality rates and provide less obvious increments to parental fitness (marginal). In an unpredictable environment, marginal offspring might in fact be raised if breeding conditions turn out to be favorable (Lack 1947). This “brood reduction” hypothesis finds support in many bird species (e.g., Drummond et al. 1986; Drummond and García Chavelas 1989) and other taxa (Mock and Parker 1997), and marginal offspring can also provide reproductive insurance against failure of the core offspring (Forbes et al. 2002), opportunities for progeny choice and adoption into other nests (Humphries et al. 2006), and food items for core offspring (Mock and Parker 1997). In obligately siblicidal species, in which brood size is trimmed under all environmental conditions, production of marginal offspring could benefit parents in each of these ways except enlargement of final brood size, and field data have detected such benefits, primarily the insurance benefit (Cash and Evans 1986; Humphries et al. 2006).

A comprehensive evaluation of natural selection on reproductive insurance requires consideration of the cost of the insurance as well as the benefit (Forbes and Lamey 1995;

Lamey et al. 1996), and little is known of the cost side of the balance sheet. Many bird species raise only one offspring per reproductive attempt, and all experience some developmental failures of their core offspring, yet few of these species produce a marginal offspring whose value is principally that of insurance. This failure to realize the reproductive insurance value of marginal offspring implies either that these species are unable to produce marginal offspring or that the cost of producing marginal offspring exceeds the benefit. Data from booby and gannet species (Family Sulidae) that raise only one chick support the latter. Costs of egg production appear to be similar for all species, and those species that would enjoy the largest insurance benefit, because their hatching failure rates are high and so are most likely to have larger benefits than costs, are the species that produce marginal offspring (Anderson 1990). Within-species studies show that only some mothers in obligately siblicidal species lay 2-egg clutches (Gargett 1971; Woodward 1972; Anderson 1990); the failure of the other parents to capitalize on the insurance potential of marginal offspring implies a prohibitive cost of egg production rather than an absolute constraint on production of second eggs. However, the nature of these inferred costs remains largely unstudied.

In this paper, we examine demographic costs and benefits of reproductive insurance in Nazca boobies (*Sula granti*), for which the insurance value of a second egg is well established (Anderson 1990; Clifford and Anderson 2001a; Humphries et al. 2006). A variable proportion of our study population lays a second egg each season and that proportion is positively correlated with the relative size of the second eggs produced in that season, suggesting that some variable environmental factor affects egg production, increasing the relative physiological effort to produce second eggs in some years (Anderson 1995). Supplemental feeding of laying mothers induces

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almost all of them to lay a second egg, suggesting that food intake is that factor (Clifford and Anderson 2001b). We use data from our long-term study of Nazca boobies and multi-state mark–recapture models to test the hypothesis that the physiological demands of producing second eggs induce future demographic costs, reducing survival and/or fecundity.

Hypotheses

Regarding the effect of insurance state (clutch size) on survival and future breeding, the “cost of reproductive insurance” hypothesis predicts that parents producing a second egg will incur costs that reduce survival and/or fecundity in the future, whereas parents of 1-egg clutches and nonbreeders should avoid those costs. Survival of parents laying 2 eggs could be lower than that of parents in lower insurance states in this case. Likewise, transitions from 2-egg to nonbreeder status would be more likely than transitions from 1-egg to nonbreeder status under this hypothesis (Figure 1A). An alternative view (the “parental quality” hypothesis) predicts that transitions between insurance states are rare because the most competent birds both breed well and survive well, the least competent do neither well, and individuals retain their ranking of intrinsic quality over time (Figure 1B). In addition, insurance status should either have no bearing on survival under the parental quality hypothesis or have an increase in survival for parents producing an insurance egg—high-quality birds may be able to produce insurance eggs and support their own survival as well. Apparent variability in parental quality was detected in a previous study by our research group: parents laying 2 eggs had higher probabilities of raising a hatched chick than did parents laying 1 egg, indicating a positive correlation between 2 components of parental care (Clifford and Anderson 2001a). We use multistate mark–recapture modeling (detailed in Methods) to test these hypotheses.

Regarding the effect of insurance state on current breeding success, the “insurance egg hypothesis” (Dorward 1962) predicts that parents laying 2-egg clutches have higher fledging success from that clutch than do parents of 1-egg clutches due to the insurance value of the second egg. The parental quality hypothesis predicts the same pattern, but the cause of the difference is overall parental quality not the insurance effect. We used 2 approaches involving logistic regression (one based on the information-theoretic [I-T] approach and model selection [Burnham and Anderson 2002] and one using traditional hypothesis testing and iterative fitting) to discriminate between these hypotheses.

METHODS

Study site and field methods

Since 1984, our group has studied the population of Nazca boobies nesting at Punta Cevallos, Isla Española, Galápagos Islands (1°23'S, 89°37'W), Ecuador. Anderson and Ricklefs (1987) and Huyvaert and Anderson (2004) provide details of the study site. Approximately 3500 Nazca booby pairs breed seasonally at the study site (Anderson 1993), with egg laying beginning in September/October and most young reaching independence by June. Only one chick is raised per year (Humphries et al. 2006). Within the Punta Cevallos study site, the team has banded a subset of young of the year and adults with aluminum US Fish and Wildlife Service bands or stainless steel bands since 1985, allowing permanent individual recognition (band loss is negligible [Huyvaert and Anderson 2004]). Annual band resight surveys have been conducted at the beginning of each breeding season since then, resulting in an extensive resight survey database. Of birds present during

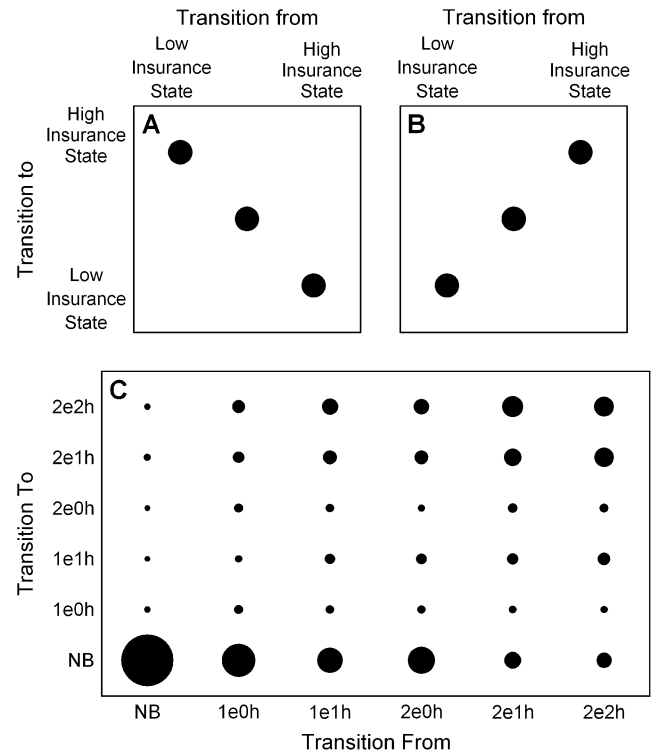


Figure 1

Bubble plots showing transition probabilities (proportional to size of bubble) between insurance states across consecutive years. In all cases, insurance state increases away from the origin. (A) Predicted negative relationship under the cost of insurance hypothesis. (B) Predicted positive relationship under the parental quality hypothesis. (C) Observed relationship in Nazca boobies (numerical values are available in Online Supplementary Material).

surveys, >99% are typically detected (Huyvaert and Anderson 2004).

Reproduction of birds nesting at the study site has been monitored in detail since 1992. Each breeding season, all nests with at least one banded parent were visited daily until the reproductive attempt of the breeding pair ended (egg was permanently abandoned, nestling died, or nestling fledged). Nazca boobies have exceptionally low breeding dispersal (Huyvaert and Anderson 2004) and so are found within our study site throughout their breeding career; thus, we consider the reproductive histories for each banded bird to be complete during our period of interest (1992–2000).

Analytical approach

Nichols et al. (1994) and Nichols and Kendall (1995) introduced the use of multistate mark–recapture models, originally developed by Arnason (1973), to examine questions in evolutionary ecology and conservation biology. Applications of these models have been focused on evaluating the effects of reproduction and migration (or movement between habitats) on organismal survival, with the goal of understanding the role of natural selection in the evolution of life-history traits (Spendelov et al. 1995; Viallefont et al. 1995; Cam et al. 1998; Doligez et al. 2002). We build on the work of Nichols et al. (1994), Nichols and Kendall (1995), Viallefont et al. (1995), and Cam et al. (1998) using multistate mark–recapture models to evaluate costs of reproductive insurance, in particular any effect of production of second eggs on future survival and on transitions between insurance states (clutch sizes of 1 or 2,

Table 1
Insurance states appearing in models

State variable code	Description	Abbreviation
0	Not seen	—
1	Seen, not reproductive	—
2	Laid single egg that did not hatch	1e0h
3	Laid single egg that hatched	1e1h
4	Laid 2 eggs, neither hatched	2e0h
5	Laid 2 eggs, 1 hatched	2e1h
6	Laid 2 eggs, 2 hatched	2e2h

hatching of 0, 1, or 2 eggs). Transitions among insurance states are analogous to changes in fecundity from one breeding season to the next and can indicate fecundity costs. For example, females that lay and hatch 2 eggs have a higher fecundity (state 6, Table 1) than do those laying 1 egg and hatching none (state 2, Table 1), so a high probability of moving from state 6 in one year to state 2 in the next would indicate a fecundity cost of reproduction from producing insurance.

Modern mark–recapture modeling relies on an I-T approach, enabling the selection of one model, from a set of candidate models, for which the least information is lost when it is used to approximate the data. Candidate models are ranked with an index such as the Akaike information criterion (AIC), which trades off model fit against model parsimony. The AIC, and in general the I-T approach encompassing the AIC, has been adopted by many biologists using mark–recapture techniques, and it is the standard model selection method in Program MARK (White 2003) and other mark–recapture analysis software. In this paper, we broaden application of the AIC to test for an effect of insurance state on fitness, selecting from a set of logistic regression models of breeding success, to complement the separate mark–recapture modeling of costs of insurance. We also conduct parallel selection of breeding success models using ubiquitous iterative-fitting, null hypothesis–testing approaches and compare the results of the 2 approaches to evaluate their relative utilities in detecting weak signals.

Multistate mark–recapture models to assess costs of insurance

Resight and breeding databases for females were assembled into 989 distinct encounter histories; the effective sample size, total number of captures or recaptures, was 3944. Only data from females were used because they are more likely to incur the costs of producing an insurance egg (males do not courtship feed). We used Program MARK (White and Burnham 1999; White 2003) to fit multistate models and to generate maximum likelihood estimates of relevant demographic parameters.

A set of candidate models was developed to evaluate the effect of insurance state (Table 1) on probabilities of survival and transition between states. Temporal variability in the dependent variables was permitted in some models. The recapture probability (P) was considered a nuisance parameter; we made the simplifying and biologically sound assumption that both insurance state and temporal variability in the environment would affect the recapture probability (as indicated by Townsend and Anderson 2007). For model selection, an I-T approach based on the AIC was used (sensu Burnham and Anderson 2002).

Table 2
Set of candidate models for testing the cost of reproductive insurance

Model reference	Model	Description
A	$S(i) P(i^* t) \Psi(i)$	Survival and transition probability vary with insurance state, consistent with costs of reproductive insurance
B	$S(i) P(i^* t) \Psi(t)$	Survival probability varies with insurance state, consistent with survival cost of reproductive insurance
C	$S(t) P(i^* t) \Psi(i)$	Transition probability varies with insurance state, consistent with fecundity cost of reproductive insurance
D	$S(t) P(i^* t) \Psi(t)$	Survival and transition probability vary with time, inconsistent with cost of reproductive insurance
E	$S(\cdot) P(i^* t) \Psi(\cdot)$	Negligible variability in survival and transition probability. Null hypothesis
F	$S(i^* t) P(i^* t) \Psi(i^* t)$	Survival and transition probability vary with insurance state and time, consistent with costs of reproductive insurance that vary with time. This is the global or umbrella model for all other models

The candidate models, following the notation of Lebreton et al. (1992) and Nichols et al. (1994), are listed in Table 2; in the candidate models, the effect of insurance state (i) is compared with the effect of temporal variability (t) on survival probability (S) and transition probability (Ψ). The best choice model from the candidate set would indicate whether insurance state contributed to a plausible explanation for the observed variability in survival or transition probability. If the best choice model included insurance state effects in transition probability, then maximum likelihood parameter estimates would determine the direction and magnitude of the association of insurance state with future performance (Figure 1A,B).

We used the methodology for goodness-of-fit testing described by Pradel et al. (2003, 2005) and the U-CARE 2.2 software (Choquet et al. 2005). The results showed that the data for our global model (Table 2, Model F) differed significantly from what would be expected with a standard JMV model ($\chi^2 = 992.2$, $P < 0.001$, degrees of freedom = 442; details in Online Supplementary Material). We attributed the lack of fit to overdispersion and calculated a variance inflation factor, $\hat{c} = 2.24$, which was applied to the AIC values of the candidate model set and interval estimates of the best model (as described in Burnham and Anderson 2002).

Two approaches for assessing breeding success

Hatchling Nazca boobies were considered to have reached independence at the approximate age of 160 days if they survived long enough to attain juvenile plumage (at ~100 days; Humphries et al. 2006); offspring survival approaches 100% after attaining juvenile plumage (Humphries et al. 2006). Breeding success declines as the breeding season progresses (Clifford and Anderson 2001a), so for this analysis females

were placed in a lay date class based on the lay date of their first egg: “early” females laid on or before the median date for that breeding season and “late” females laid after. The lay date for the minority of eggs laid before the field crews arrived during a given breeding season was estimated by subtracting 43 days (average incubation period; Anderson 1993) from the egg’s hatch date.

We used logistic regression models to test the effect of insurance state, breeding season (year, equivalent to t in multi-state mark–recapture models), and lay date class on the binary dependent variable breeding success, coded 1 (produced a fledgling) or 0 (did not produce a fledgling). Two different models of breeding success were developed: one set in which all reproductive insurance states (clutch sizes of 1 or 2, hatching of 0, 1, or 2 eggs—1e0h, 1e1h, 2e0h, 2e1h, and 2e2h) were included in the data set and another set including only those states that included a hatchling (1e1h, 2e1h, and 2e2h). In the first model set, the effect of having an insurance egg was compared with not having an insurance egg by comparing breeding success of 1-egg to 2-egg states. The second model set included only cases in which at least 1 egg hatched. In the first set, the effect of insurance on breeding success was mediated by the insurance effect on hatching success (i.e., insurance increases the probability of successfully hatching an egg and therefore increases the probability of successful breeding). In the second set, the hatching success effect on breeding success was removed, and any effects of parental quality/experience on clutch size and posthatching parental care are featured.

Logistic regression models were developed using SAS Proc LOGISTIC for the iterative-fitting approach and SAS Proc GENMOD (SAS 2001) for the I-T approach. For the iterative-fitting approach, explanatory variables were added in a step-wise fashion and the statistical significance of the additional variables was tested, until a final set of statistically significant explanatory variables was established. Conversely, for the I-T approach, a set of biologically meaningful candidate models was developed (Table 3), and the model with the highest AIC weight, an index of relative plausibility, was taken to indicate which factors influenced breeding success (Burnham and Anderson 2002).

RESULTS

Costs of reproductive insurance

The multistate model that included the effect of insurance state on transition probability between breeding states, but not on survival probability, was the best choice model in the candidate set (Table 4). The fact that the model based on insurance state fits the data better than a model based on time (temporal variability in the environment) indicated that insurance state influenced transition probability and was a more important effect on transition probabilities than were tempo-

Table 3
Set of candidate models for testing the benefit of reproductive insurance

Model reference	Model	Model description
A	State	Breeding success varies by insurance
B	Year	Breeding success varies by breeding season (1992–1999)
C	Lay class	Breeding success varies by lay class (early vs. late)
D	State, year	Breeding success varies by insurance state and breeding season
E	State, lay class	Breeding success varies by insurance state and lay class
F	Year, lay class	Breeding success varies by breeding season and lay class
G	State, year, lay class	Breeding success varies by insurance state, breeding season, and lay class

ral factors. The representation of the 5 states in the annual pool varied markedly across years (Figure 2); the nature of the association between insurance state and transition probability is shown in Figure 1C. Females that laid 2 eggs and hatched at least one were more likely to remain at the 2-egg state than to change to a lower state, and females laying 1 egg were more likely to change to a lower state (nonbreeder) than to a higher state (2-egg). Nonbreeders were most likely to remain nonbreeders. The cost of insurance hypothesis predicts more transitions to lower states by high-effort females than by low-effort females. This prediction is generally contradicted by the transition probabilities of nonbreeding, 1-egg, and 2-egg females, excepting 2-egg females that hatched no eggs (Figure 1C): 2-egg females that hatched at least 1 egg had the lowest probabilities of laying only 1 egg or not breeding in the following year. The parental quality hypothesis predicts that females maintain their insurance state. This prediction was partially supported: females laying 2 eggs tended to continue laying 2 eggs and nonbreeders tended to remain nonbreeders; however, most 1-egg females changed to nonbreeder or (less frequently) 2-egg status (Figure 1C).

Benefits of reproductive insurance

Logistic regression analyses of breeding success using model selection based on 1) an I-T logistic approach and 2) iterative fitting approach for the first model set (where state refers to insurance [2-egg clutch] or no insurance [1-egg clutch]) both yielded a top-ranking model with year, lay class, and insurance state effects (Table 5). Maximum likelihood estimates of breeding success associated with 1- and 2-egg clutches were derived from the top I-T model (Figure 3). These estimates

Table 4
Model ranking for capture–recapture models involving annual survivorship and all insurance states

Model reference	Model	QAIC _c	QAIC _c Wt	Number of parameters	QDeviance
C	$S(t) P(i^* t) \Psi(i)$	7786.586	1.000	79	4155.854
A	$S(i) P(i^* t) \Psi(i)$	7809.407	0.000	78	4180.757
F	$S(i^* t) P(i^* t) \Psi(i^* t)$	7905.393	0.000	294	3800.395
D	$S(t) P(i^* t) \Psi(t)$	8246.03	0.000	56	4662.926
B	$S(i) P(i^* t) \Psi(t)$	8270.548	0.000	55	4689.503
E	$S(.) P(i^* t) \Psi(.)$	8309.423	0.000	44	4750.946

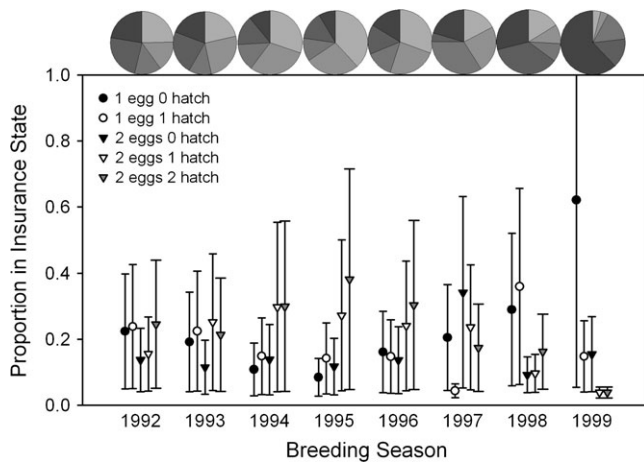


Figure 2

Proportions in each insurance state during the study period. Error bars represent 95% confidence limits. Pie charts above each year show 1 egg 1 hatch state in black for that year, with increasing insurance state proceeding counterclockwise in increasingly lighter shades of gray.

indicated a consistent advantage of 2-egg females over 1-egg females. This benefit could be due to the insurance advantage in producing hatched young in the first part of the breeding attempt and/or the known parental quality advantage of 2-egg females in raising hatched young in the chick-rearing part of the attempt (Clifford and Anderson 2001a).

The 2 approaches yielded differing results for the second model set, in which only females that produced a hatchling were included (1e1h, 2e1h, and 2e2h states). The model selected using iterative fitting (backward selection) included breeding season (Wald $\chi^2 = 318.27$, $P < 0.0001$) and lay class (Wald $\chi^2 = 22.13$, $P < 0.0001$) but not insurance state (Wald $\chi^2 = 3.07$, $P = 0.22$). In contrast, under the I-T approach (Table 6), the model that included lay class and breeding season was the best choice (AIC weight = 0.8113), and the model that included insurance with both breeding season and lay class was a good second choice (AIC weight = 0.1886; Burnham and Anderson 2002). Because these top 2 models are identified as similarly plausible and the insurance state was included in one of the top 2, the I-T approach yielded a conclusion that insurance state influenced posthatching breeding success.

Burnham and Anderson (2002) recommended model averaging to obtain parameter estimates when multiple models have appreciable AIC weights. Accordingly, our maximum likelihood estimates of breeding success included effects of insurance state, and the effect of insurance state on posthatch-

ing success was positive, but minor (Figure 4). Because the effect of insurance state must be related to posthatching performance in this test, this result indicates better chick-rearing ability in parents that laid insurance eggs, suggestive of an overall parental quality effect. However, the advantage of 2-egg females in breeding success (Figure 3) derived principally from the insurance effect of second eggs.

DISCUSSION

Our goal in this study was to test 2 hypotheses explaining the failure of some female Nazca boobies to take advantage of the fitness increment provided by insurance eggs. During this study, that proportion varied from 0.226 in the 1995 laying period to 0.767 in 1999 (Figure 2). Two previous studies concluded that parent Nazca boobies incur meaningful physiological costs from the production of insurance eggs (Anderson 1990; Clifford and Anderson 2001b), motivating a hypothesis based on a cost of insurance: females laying an insurance egg in one year should be less likely to survive to the next year, and/or be less likely to lay 2 eggs in the next year, than will females not laying insurance eggs. Parents laying insurance eggs also have higher success raising hatched chicks, suggesting that underlying parental quality helps to explain variation in clutch size (Clifford and Anderson 2001a). The 2 hypotheses make different predictions regarding parental survival and the tendency to maintain insurance state over time, and we analyzed this tendency to evaluate the relative importance of insurance costs and parental quality in the causation of clutch size variation.

Using model ranking to test the cost of insurance hypothesis, we identified the best choice model (the model that optimized the trade-off of fit and parsimony) as one in which variability in current insurance state explained variation in future insurance state, but not in survival (Table 4). This approach showed that near-term survival was affected less by production of insurance eggs than by the large set of factors associated with temporal variability in the environment and in the females themselves. It did not rule out a minor survival cost of insurance. In contrast, insurance state was associated with future fecundity (Table 5), a result that could be consistent with either the cost of insurance hypothesis (nonrandom transitions out of current insurance state) or the parental quality hypothesis (nonrandom retention of insurance state). The pattern of changes in short-term fecundity generally favored the parental quality hypothesis over the cost of insurance hypothesis because females laying 2 eggs and non-breeders tended to maintain their insurance state over time, despite incurring and not incurring, respectively, the costs of egg production (Figure 1C). In the most specific contradiction of the cost of insurance hypothesis, females in 2 of the

Table 5

Model ranking for logistic regression models of breeding success, where state refers to females that laid 1-egg clutches (no insurance) or 2-egg clutches (insurance)

Model reference	Model	AIC	AIC Wt	Number of parameters	Deviance
G	State, year, lay class	2766.4918	1.0000	14	2738.4918
D	State, year	2805.0304	0.0000	11	2783.0304
F	Year, lay class	2836.7818	0.0000	12	2812.7818
B	Year	2873.5108	0.0000	9	2855.5108
E	State, lay class	3570.1528	0.0000	5	3560.1528
A	State	3571.6358	0.0000	3	3565.6358
C	Lay class	3732.8394	0.0000	3	3726.8394

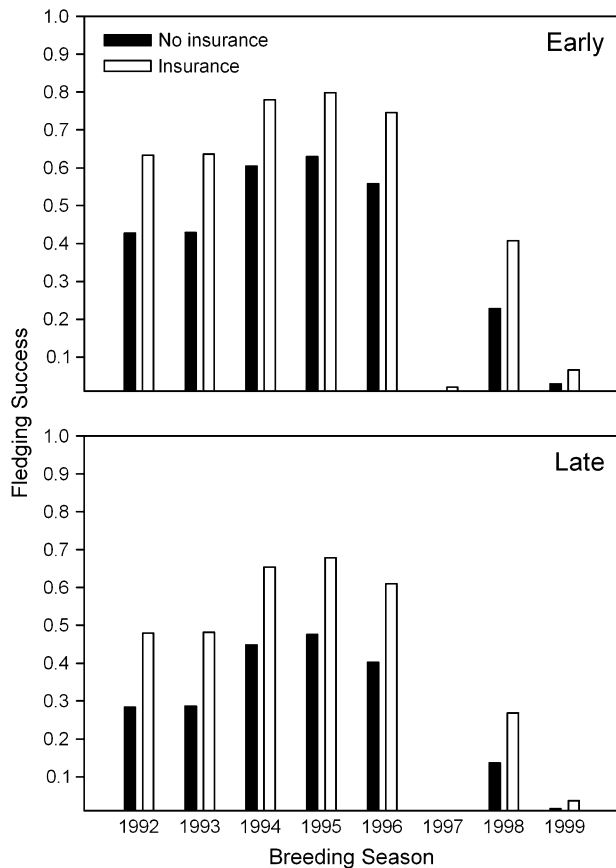


Figure 3
Maximum likelihood estimates for breeding success by breeding season, insurance state, and lay class, where state refers to production of 1-egg versus 2-egg clutches. “Early” females laid on or before the median laying date for that season, and “Late” females laid after the season’s median date.

3 insurance states involving insurance eggs (2e1h and 2e2h) tended to lay insurance eggs again in the next year, and females laying only one egg were more likely to become nonbreeders than to move to more productive insurance states involving insurance eggs.

The exception to this pattern was females in the 2e0h insurance state, which tended to drop in insurance state to nonbreeder status, consistent with the cost of insurance hypothesis (Figure 1C). However, the failure of these females to

hatch any eggs despite the redundancy of an insurance policy gives an a priori suspicion of resource limitation, illness, or other problem arising after egg laying and before hatching. The frequent transition of 2e0h females to nonbreeder status (Figure 1C) can thus be interpreted as poor performance in egg hatching and in future reproduction that are both rooted in an underlying quality deficit rather than as evidence of a cost of producing an insurance egg. Consistent with this view, females in 1-egg insurance states were similarly likely to move to nonbreeder status (Figure 1C), and females laying only 1 egg in 1996 showed an underlying quality deficit (Clifford and Anderson 2001a).

We conclude that production of insurance eggs is more strongly related to the general reproductive competence of female Nazca boobies than to a trade-off between past and current production of those eggs. This conclusion does not reject the cost of insurance hypothesis, though: a minority of 2e1h and 2e2h females changed to nonbreeder or 1-egg status and a minority of 1-egg females changed to 2-egg status (Figure 1C), as expected under this hypothesis. Furthermore, 2 previous studies both concluded that insurance eggs carry a demonstrable cost (Anderson 1990; Clifford and Anderson 2001b). Costs of insurance could accrue over a longer term than we modeled. We examined effects occurring within a year of a given breeding attempt, but the demographic effect of a given physiological investment could be manifested over a period of several or many seasons. Reproductive senescence in Nazca boobies is apparent at the approximate age of 20 years (Anderson and Apanius 2003), and this late-term decline in function might be accelerated by a history of producing insurance eggs.

In a species with a low mortality rate due to extrinsic sources, parents are expected to prioritize self-maintenance over short-term reproductive success to a greater degree than are short-lived species. This perspective provides an alternative interpretation of our results: production of insurance eggs may induce only short-term physiological costs, and females do not elect to incur those costs if the costs will have long-term demographic effects (on survival and/or fecundity). This interpretation accommodates the evidence of a physiological cost of egg production, the lack of evidence of demographic correlates of these costs, and the importance of self-maintenance for potentially long-lived organisms in life-history theory.

We suspect that parental quality and (nondemographic) insurance costs have additive effects on future clutch size. The proportion of nonbreeding females changing to breeder status is relatively low, despite access to large numbers of unpaired males in this population with a male-biased sex ratio (Townsend and Anderson 2007). These nonbreeding females are likely of such low breeding quality that they are unlikely to

Table 6
Model ranking for logistic regression models of breeding success restricted to states involving at least 1 hatched egg

Model reference	Model	AIC	AIC Wt	Number of parameters	Deviance
F	Year, lay class	1518.8526	0.8113	11	1496.8525
G	State, year, lay class	1521.7708	0.1886	14	1493.7709
B	Year	1537.7408	0.0001	9	1519.7408
D	State, year	1539.6072	0.0000	12	1515.6071
H	State, year, lay class, second-order interactions	1540.4664	0.0000	60	1420.4664
A	State	2113.2342	0.0000	4	2105.2343
E	State, lay class	2115.2178	0.0000	6	2103.2177
C	Lay class	2125.386	0.0000	3	2119.3859

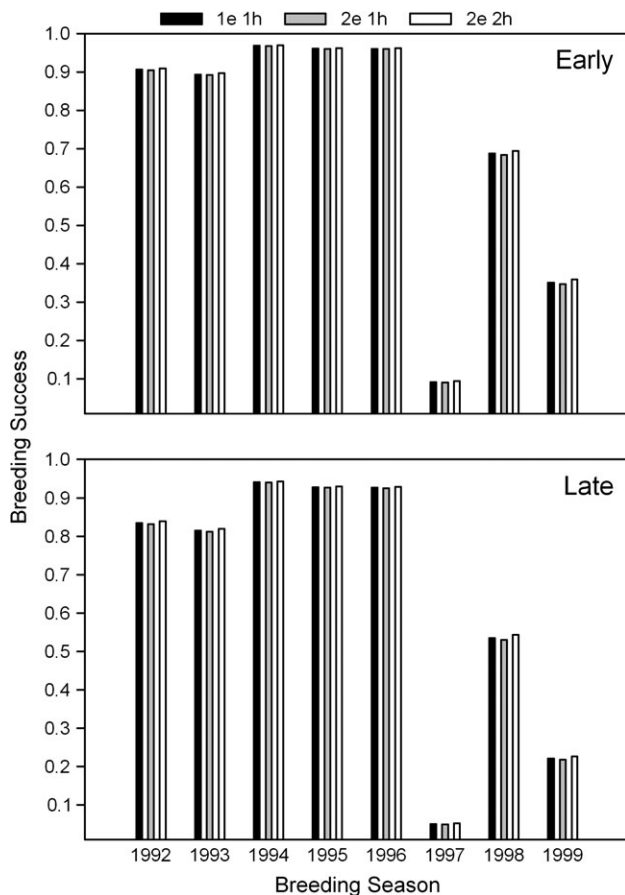


Figure 4
Maximum likelihood estimates for breeding success by breeding season, insurance state, and lay class, including only states in which at least 1 hatchling was produced.

breed in the near future under any circumstances, and the fact that they incur no insurance costs is largely irrelevant to their future egg production. Females laying 1-egg clutches frequently become nonbreeders, possibly because they have low intrinsic quality and are thus more affected in the future by costs of egg production and chick rearing than are females laying insurance eggs. Females laying insurance eggs and hatching at least one of them may experience lower costs of reproduction because their intrinsic quality is higher (i.e., Clifford and Anderson 2001a). Under this interpretation, females in the 2e1h and 2e2h insurance states produce most of the population's reproductive output because females in this state are generally at least as numerous as those in other breeding insurance states (Figure 2) and because their breeding success is higher than that of females producing 1 egg (Figure 3).

The use of multistate mark-recapture models to evaluate these hypotheses allowed robust estimates of potential costs of insurance because survival and transition probabilities (fecundity) were not confounded by detection probabilities. The use of an I-T approach allowed testing of multiple hypotheses, rather than multiple stepwise comparisons of different effects versus null models, as is the case with iterative model fitting. In addition, the I-T approach detected a faint signal, the effect of insurance state on posthatching breeding success (Table 6), that was not detected using iterative-fitting model selection. This insurance effect was previously detected in an experimental study on this system (Clifford and Anderson 2001a),

providing evidence that the I-T approach was a more sensitive tool for model comparison than was conventional iterative model fitting. The strength of this approach in detecting faint effects makes a case for use of this approach in all observational studies where bolstering of faint, but potentially important, effects through experimental manipulations cannot occur. As was the case with our breeding success models, multiple competing models may contribute partially to the explanation of natural variability. This perspective may cause some confusion, especially for investigators accustomed to the dichotomization of explanatory models imposed by traditional statistical analysis; however, it may prevent the discarding of important information in data.

In summary, we found no evidence that production of insurance eggs reduced future survival and fecundity in female Nazca boobies. Earlier experimental work (Clifford and Anderson 2001b) indicated that production of insurance eggs was food limited. Together, these studies indicate that costs of egg production limit clutch size in some females and that the threshold cost governing production of insurance eggs is below the level that would affect future performance. The costs are physiological, apparently without a demographic consequence. Rather than indicating a demographic cost of reproduction, clutch size is positively correlated within females, indicating variation in overall breeding quality. Thus, variation in production of insurance eggs has both strong environmental (Figure 2) and individual quality (Figure 1) components. However, individual quality makes only a minor contribution to breeding success apart from its effect on production of insurance eggs (Figure 3).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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REFERENCES

- Anderson DJ. 1990. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. *Am Nat.* 135:334–350.
- Anderson DJ. 1993. Masked booby (*Sula dactylatra*). In: Poole A, Gill F, editors. The birds of North America, No. 73. Philadelphia (PA): The Academy of Natural Sciences.
- Anderson DJ. 1995. The role of parents in siblicidal brood reduction of two booby species. *Auk.* 112:860–869.
- Anderson DJ, Apanius V. 2003. Actuarial and reproductive senescence in a long-lived seabird: preliminary evidence. *Exp Gerontol.* 38:757–760.
- Anderson DJ, Ricklefs RE. 1987. Radio-tracking masked and blue-footed boobies (*Sula spp.*) in the Galápagos Islands. *Natl Geogr Res.* 3:152–163.
- Arnason AN. 1973. The estimation of population size, migration rates and survival in a stratified population. *Res Popul Ecol.* 13:97–113.
- Burnham KP, Anderson DR. 2002. Model selection and inference: a practical information-theoretic approach. New York: Springer-Verlag.

- Cam E, Hines JE, Monnat JY, Nichols JD, Danchin E. 1998. Are adult nonbreeders prudent parents? The Kittiwake model. *Ecology*. 79: 2917–2930.
- Cash KJ, Evans RM. 1986. Brood reduction in the American white pelican (*Pelecanus erythrorhynchos*). *Behav Ecol Sociobiol*. 18:413–418.
- Choquet R, Reboulet A–M, Lebreton J–D, Gimenez O, Pradel R. 2005. U–CARE 2.2 User's manual. Montpellier (France): CEFÉ.
- Clifford LD, Anderson DJ. 2001a. Experimental demonstration of the insurance value of extra eggs in an obligately siblicidal seabird. *Behav Ecol*. 12:340–347.
- Clifford LD, Anderson DJ. 2001b. Food limitation explains most clutch size variation in the Nazca booby. *J Anim Ecol*. 70:539–545.
- Doligez B, Clobert J, Pettifor RA, Rowcliffe M, Gustafsson L, Perrins CM, McCleery RH. 2002. Costs of reproduction: assessing responses to brood size manipulation on life-history and behavioural traits using multi-state capture-recapture models. *J Appl Stat*. 29:407–423.
- Dorward DF. 1962. Comparative biology of the white booby and the brown booby *Sula* spp. at Ascension. *Ibis*. 103b:174–200.
- Drummond H, García Chavelas CG. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Anim Behav*. 38:806–819.
- Drummond H, González E, Osorno JL. 1986. Parent-offspring cooperation in the blue-footed booby (*Sula nebouxi*): social roles in infanticidal brood reduction. *Behav Ecol Sociobiol*. 19:365–372.
- Forbes LS, Lamey TC. 1995. Insurance developmental accidents, and the risks of putting all year eggs in one basket. *J Theor Biol*. 180:247–256.
- Forbes S, Grosshans R, Glassey B. 2002. Multiple incentives for parental optimism and brood reduction in blackbirds. *Ecology*. 83:2529–2541.
- Gargett V. 1971. Some observations on black eagles in the Matopos, Rhodesia. *Ostrich*. 9(Suppl):91–124.
- Humphries CA, Fischer KL, Arevalo D, Anderson DJ. 2006. Contributions of marginal offspring to reproductive success of Nazca boobies (*Sula granti*): tests of multiple hypotheses. *Oecologia*. 147:379–390.
- Huyvaert KP, Anderson DJ. 2004. Limited dispersal by Nazca boobies. *J Avian Biol*. 35:46–53.
- Lack D. 1947. The significance of clutch size I, II. *Ibis*. 89:302–352.
- Lamey TC, Evans RM, Hunt DJ. 1996. Insurance reproductive value and facultative brood reduction. *Oikos*. 77:285–290.
- Lebreton J, Burnham KP, Clobert J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr*. 62:67–118.
- Mock DW, Forbes LS. 1995. The evolution of parental optimism. *TREE*. 10:130–134.
- Mock DW, Parker GA. 1997. The evolution of sibling rivalry. Oxford: Oxford University Press.
- Nichols JD, Hines JE, Pollock KH, Hinz RL, Link WA. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. *Ecology*. 75:2052–2065.
- Nichols JD, Kendall WL. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. *J Appl Stat*. 22:835–846.
- Pradel R, Gimenez O, Lebreton J–D. 2005. Principles and interest of GOF tests for multistate capture-recapture models. *Anim Biodivers Conserv*. 28:189–204.
- Pradel RC, Wintrebert MA, Gimenez O. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics*. 59:43–53.
- SAS Institute. 2001. SAS/STAT Software. Cary (NC): SAS Institute.
- Spendlow JA, Nichols JD, Nisbet IC, Hays H, Cormons D, Burger J, Safina C, Hines JE, Gochfeld M. 1995. Estimating annual survival and movement rates of adults within a metapopulation of Roseate terns. *Ecology*. 76:2415–2428.
- Townsend HM, Anderson DJ. Forthcoming 2007. Assessment of costs of reproduction in a pelagic seabird using multi-state mark-recapture models. *Evolution*.
- Viallefont A, Cooch EG, Cooke F. 1995. Estimation of trade-offs with capture-recapture models: a case study on the lesser snow goose. *J Appl Stat*. 22:847–891.
- White GC. 2003. Program MARK [Internet]. [cited 2007 July 15]. Fort Collins (CO): Colorado State University; Available from: <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>.
- White GC, Burnham KP. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*. 46(Suppl): 120–138.
- Woodward PW. 1972. The natural history of Kure Atoll, northwest Hawaiian islands. *Atoll Res Bull*. 164:1–318.