

ASSESSMENT OF COSTS OF REPRODUCTION IN A PELAGIC SEABIRD USING MULTISTATE MARK–RECAPTURE MODELS

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We used a long-term population band-resight survey database, a parallel reproduction database, and multistate mark–recapture analysis to assess the costs of reproduction, a keystone concept of life-history evolution, in Nazca boobies (*Sula granti*) from Punta Cevallos, Isla Española, Galápagos, Ecuador. We used eight years of resight and breeding data to compare models that included sex- and state-specific survival probabilities and probabilities of transition between reproductive states using multistate mark–recapture models. Models that included state-specific effects were compared with models lacking such effects to evaluate costs of reproduction. The top model, optimizing the trade-off of model simplicity and fit to the data using the Akaike Information Criterion (AIC), showed evidence of a temporally varying survival cost of reproduction: nonbreeders showed higher annual survival than breeders did in some years. Because increasing investment among breeders showed no negative association with survival and subsequent breeding success, this evidence indicates a cost to both males and females of initiating, but not of continuing, a reproductive attempt. In some cases, breeders reaching the highest reproductive state (fledging an offspring) showed higher survival or subsequent breeding success than did failed breeders, consistent with differences in overall quality that promote both survival and reproduction. Although a male-biased adult sex ratio was observed in this population of Nazca boobies, models of state- and sex-specific survival and transition probabilities were not supported, indicating that males and females do not incur different costs of reproduction, and that the observed sex ratio bias is not due to sex-specific adult mortality.

KEY WORDS: Galápagos, life-history theory, sex ratio, sex-specific survival, statistical model.

Trade-offs due to constraints on simultaneous evolution of linked traits are a keystone concept of life-history theory. However, a clear demonstration of trade-offs and consequences of trade-offs is often elusive because of confounding variables and study artifacts. The most thoroughly studied trade-offs are those which affect fitness directly through survival and reproduction. Williams (1966) formalized theory about reproductive trade-offs by demonstrating that iteroparous organisms maximize reproductive rate by optimizing allocation of effort between current and future reproduction. The cost of current reproduction is paid through a decrease

in future reproduction via (1) reduced survival (i.e., survival costs of reproduction) and/or (2) reduced future fecundity (fecundity costs of reproduction; Stearns 1992). In this paper, we use a novel (for evolutionary biologists) technique and long-term serial data to evaluate a key trade-off, the cost of reproduction, in a long-lived seabird, and the potential for the cost of reproduction to affect the adult sex ratio (ASR). Specifically, we use a robust, quantitative approach to examine both survival and fecundity costs of reproduction with multistate mark–recapture models (Nichols 1992).

Numerous researchers have estimated the cost of reproduction, or failed to detect such costs, but methodological issues and confounding variables undermine some results. Reznick (1989, 1992) and Lindén and Møller (1989) classified several different methods for demonstrating costs and their relative value in

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determining whether a cost of reproduction has been demonstrated for a particular species. Reproductive costs may be detected through (1) experimental manipulation (such as changing brood size and measuring effects on parent survival and future fecundity) and (2) observations in natural settings in which the normal selective regime is not altered. Experimental studies can control confounding variables such as parental quality; however, they are often short-term and have a limited scope, so effects of environmental variability may be poorly controlled. Conversely, observational studies typically do not control parental quality; however, external sources of variability become evident. An ideal study of reproductive costs would include experimental and observational work on a study system. Many experimental studies of costs of reproduction have been conducted using birds (e.g., Lindén and Møller 1989; Stearns 1992), presenting contradictory results. Some of the inconsistency may be attributable to study artifacts, such as artificial inflation of population density and density-dependent feedbacks by the presence of artificial nests (Lindén and Møller 1989) or other habitat alterations.

In addition, assessing survival costs of reproduction presents some difficulties. Survival measurements may be confounded by covariance between encounter probability and reproductive status. For example, reproductive status may influence nest site attendance and so the amount of time an animal spends in the resight area, thus influencing the encounter probability.

MULTISTATE MODELS TO ESTIMATE REPRODUCTIVE COSTS

Although the existence of reproductive costs is logically compelling, an accurate empirical assessment of reproductive costs has proved elusive for many species because of confounding factors. In this paper, we present an expansion of a novel technique for evaluating reproductive costs that accounts for at least some of these factors, exploiting the power of recent advances in Cormack–Jolly–Seber (CJS) mark–recapture (resight) models (Pollock et al. 1990; Nichols 1992; Lebreton et al. 1993). Specifically, we expand on the techniques described by Nichols et al. (1994), Nichols and Kendall (1995), Viallefont et al. (1995), and Cam et al. (1998) to estimate survival costs of reproduction with multistate capture–recapture models. In essence, the sequence of events in an individual's life history can be viewed as the realization of a Markov process; for example, the probability of an organism breeding during season x is conditional on the probability of breeding during season $x - 1$. Basic multistate mark–recapture models are based on first-order Markov processes, and thus can be readily adapted to quantify costs of reproduction. These techniques account for any interaction between breeding status and detection and survival probability of individuals.

Models with stratification can be compared with constrained, unstratified models to test hypotheses about population genetics

and evolutionary ecology of the populations of interest (Arnason 1973; Brownie et al. 1993; Nichols and Kendall 1995). The method suggested by Nichols et al. (1994) includes developing a general model in which survival probabilities at time i for breeders (state 1) versus nonbreeders (state 2) are allowed to differ [$S(1) S(2)$]. This general model is then compared with a constrained model, which is effectively a null-hypothesis model, with survival probabilities constrained to be equal [$S(1) = S(2)$]. The better model is selected based on the Akaike Information Criterion (AIC; Burnham and Anderson 2002; Yoccoz et al. 2002). If the constrained model has an appreciably higher AIC weight than the unconstrained model, then it is a superior model based on the optimized trade-off of model simplicity and fit, and a survival cost of reproduction is not indicated. If the general model has a higher AIC weight, and the survival estimates for nonbreeders based on this top model are higher than for breeders, then a survival cost of reproduction is indicated. Similarly, state transition probabilities can be constrained or left unconstrained to test effects of current versus future reproduction.

This multimodel inference using multistate mark–recapture models exploits the rich information content of large, long-term demographic datasets to provide a sensitive investigative tool. Such sensitivity may be required to detect costs of reproduction in long-lived organisms like pelagic seabirds, whose demography should favor low cost ceilings on reproductive effort (Goodman 1974).

CONSEQUENCES OF REPRODUCTIVE COSTS

In addition to using the methods of Nichols et al. (1994) to assess phenotypic reproductive costs, we expand on the methods to investigate sex ratio bias. Trivers (1972) and Breitwisch (1989) predicted male-biased sex ratios in monogamous birds with biparental care if egg production induces higher levels of parental investment by females than by males. All else being equivalent (i.e., parental effort in brooding and chick-rearing), the excess cost of reproduction is expected to cause lower female survival and a male-biased ASR. Breitwisch (1989) demonstrated that in biparental, monogamous birds: (1) male-biased ASRs are widespread; (2) the bias arises after a breeding season; and (3) sex-specific mortality occurs in the nonbreeding season, with females suffering higher mortality. These results suggest a delayed payment for parental investment. Pugesek and Wood (1992) and Pugesek et al. (1995) also provided some evidence of females paying a higher cost of reproduction; however, Tavecchia et al. (2001) suggested that evidence for females paying higher survival costs of reproduction is equivocal. By considering sex-specificity and stages of reproduction (i.e., egg production, hatching, and fledging), we test the hypothesis that a male-biased ASR is associated with decreased female survival or fecundity attributable to investment in egg production or other investment that females make in excess.

Using a 14-year mark–resight database and an 8-year reproduction database of Nazca boobies (*Sula granti*) from the Galápagos Islands, Ecuador, we adapt the methods of Nichols et al. (1994) to evaluate reproductive costs. In our mark–recapture models, state designates the highest reproductive level attained (nonbreeder, egg, nestling, fledgling) by a bird in a given annual breeding season, and birds that produce fledglings are considered to have reproduced successfully. In addition, we test for sex specificity in costs incurred. Thus, we are able to determine if costs of reproduction are sex-specific, as well as to consider temporal variability in these costs.

We designed multistate models that included and excluded reproductive state and sex as factors explaining survival and state transition probability, which we consider to be a measure of short-term (annual) changes in fecundity, and compared multiple hypotheses simultaneously to determine which model best described the data. A global, or unconstrained, model represented a hypothesis of sex- and state-specific effects on survival and fecundity, and a constrained, or unstratified, model represented a hypothesis of no sex- or state-specific effects on survival and fecundity and thus, no observed survival or fecundity costs of reproduction. Models that included state-specific effects on survival or fecundity were only considered to have indicated survival and fecundity costs of reproduction if the parameter estimates were consistent with such an explanation. That is to say, a lower survival rate for breeders than for nonbreeders would be consistent with a cost of reproduction, or successful breeders subsequently becoming nonbreeders or unsuccessful breeders more frequently than nonbreeders did. Individual parental quality effects might explain the converse result.

By studying an undisturbed Nazca booby population breeding on a remote, uninhabited island of the Galápagos archipelago, we were able to circumvent many effects that have confounded other field studies examining costs of reproduction. The extent to which human intervention or habitat alteration has affected the system is minimal. In addition, Nazca boobies are monogamous, long-lived seabirds, with both parents providing care (Anderson 1993; Anderson and Apanius 2003), so sex-specific reproductive costs are readily measured. The open habitat and indifference of these Galápagos birds to humans also improve detection (recapture) probability, increasing precision in survival estimates over that in less tractable systems.

Materials and Methods

STUDY AREA AND FIELDWORK

We studied Nazca booby nesting biology at Punta Cevallos, Isla Española, Galápagos Islands (1°23'S, 89°37'W), Ecuador between 1985 and 2000 in conjunction with other long-term research on this species. Anderson and Ricklefs (1987) and Huyvaert and

Anderson (2004) provide details of the study site. Approximately 3500 Nazca booby pairs breed at Punta Cevallos (Anderson 1993), with eggs laid from October to February and fledging occurring from March until June. Within the Punta Cevallos study site, we have captured and banded a subset of young of the year and adult Nazca boobies with aluminum U.S. Fish and Wildlife Service bands or stainless steel bands since 1984. Since 1992, primarily nestlings have been banded, thus banding cohort is roughly correlated with age. The subset of birds banded each year was from the same area within Punta Cevallos. An annual band resight survey (“annual BRS”) at the beginning of the breeding season has been conducted in this area since 1985, yielding a resight survey database. A previous analysis indicated that the detection rate for these birds is greater than 90%, that is, over 90% of banded birds that are in the colony at some time in a given breeding season are detected during band resight surveys (D. J. Anderson, unpubl. data). Of birds present during the short period of the survey, > 99% are typically detected (Huyvaert and Anderson 2004).

Similarly, the reproduction of birds nesting in the study site has been monitored since 1992 via daily visits until the reproductive attempt of the breeding pair ended (the egg was abandoned and a parent did not return for more than 10 days, the nestling died, or the nestling fledged). Offspring were considered to have fledged successfully, that is, reached independence at approximately age of 160 days, if they survived long enough to attain juvenile plumage (at approximately 100 days). Nest histories were compiled from all nests in one part (the “Study Area”) of the study site each year, providing a representative sample of nest histories for comparison across years. Outside the Study Area, only nests with at least one banded parent were monitored.

Surveys of breeding Nazca boobies in other islands in the Galápagos and just outside our study area at Punta Cevallos indicated an exceptionally low degree of breeding dispersal (Huyvaert and Anderson 2004). Virtually none of the birds banded by our group have bred on other islands or outside of areas monitored by our group on Isla Española, and once they settled in our study site, they have not bred elsewhere (Huyvaert and Anderson 2004). Because site fidelity is virtually 100%, we refer to apparent survival estimates as survival in our mark–recapture analysis. The breeding colony is open, so all nests are readily apparent, and overlooking a nesting attempt is improbable. Thus, it is likely that we have compiled complete reproductive histories for each banded bird nesting in the study site during our period of interest (1992–2000).

NAZCA BOOBY LIFE HISTORY

The Nazca boobies of the Galápagos have previously been classified as masked boobies (*Sula dactylatra granti*); however, recent analyses of morphological, breeding, and behavioral data (Pitman and Jehl 1998), and of mitochondrial DNA haplotypes (Friesen et al. 2002) suggest that populations in the Galápagos archipelago

and other nearby populations on the Nazca tectonic plate should be considered a separate biological species. Under revised nomenclature (AOU 2000), these birds are referred to as Nazca boobies (*S. granti*).

The breeding ecology of Nazca boobies is well known due to extensive studies in the Galápagos by Nelson (1978) and Anderson (1993) and colleagues. The colonial breeding habit, indifference of these birds to humans, and open habitat in the Galápagos facilitate field studies. Mated Nazca boobies lay one or two eggs, but raise a maximum of one chick per year. If two eggs hatch, obligate siblicide reduces the brood to a single offspring within days of hatching (Anderson 1989; Humphries et al. 2006). The population at this site showed high breeding success during the first five years of this study (the 1992–1993 through 1996–1997 breeding seasons; Fig. 1). The 1997–1998 breeding season occurred during an El Niño–Southern Oscillation (ENSO) event, with attendant general breeding failure but a normal amount of nest initiation (Clifford and Anderson 2001). Following the end of the ENSO in mid-1998, breeding success was also low during the 1998–1999 and 1999–2000 seasons (Fig. 1). Most breeding failure is due to starvation (Nelson 1978; Anderson 1993) and attacks by nonbreeding adults when both parents are absent on feeding trips (Anderson et al. 2004). Predation accounts for less than 1% of failures (Anderson 1993).

Male and female mates, which are readily distinguished by whistling and honking voices, respectively (Nelson 1978), share parental care from the beginning of egg incubation until the fledging or death of the offspring. Parents provision nestlings by flying to pelagic feeding grounds (75 km from the colony in the case of Anderson and Ricklefs 1987) during trips of several hours to days

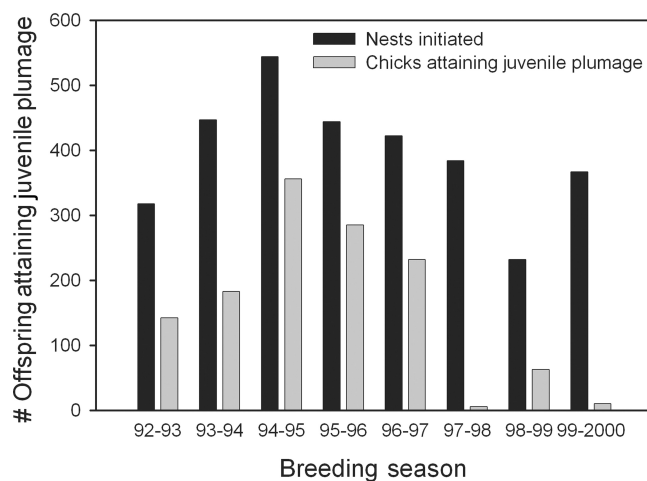


Figure 1. Breeding parameters from a subpopulation in the Study Area (see Materials and Methods) providing a random sample (including both banded and unbanded birds) of reproductive performance in each year of the study.

(Anderson and Ricklefs 1992). Adult females are 15.6% heavier than males (Anderson 1993). Species that exhibit sexual size dimorphism (SSD) provide useful opportunities to study sex ratios and sex allocation, because the potentially higher energetic requirements of the larger sex could influence survival. In the case of Nazca boobies, mothers also bring larger loads of food to offspring (Anderson and Ricklefs 1992) and spend more time foraging during the nestling period (V. Apanius, M. A. Westbrook, and D. J. Anderson, unpubl. ms.). Mothers potentially pay higher energetic (and nutrient) costs than males do early in the breeding season due to egg production; males do not courtship-feed. Finally, females breed more frequently than males do (Maness and Anderson), so females incur any costs of reproduction more frequently.

DATA IN SUPPORT OF MODELING

We assembled our resight and breeding databases into encounter histories as horizontally structured encounter-history-type files (White and Burnham 1999) with a bird's unique identifying band number as the case identifier and the bird's sex dummy coded. Variables coding each bird's presence and breeding state in a given year completed the file. These performance variables were coded 1 ("state 1") for nonbreeding birds encountered during the year's annual survey, 2 for birds that produced eggs that did not hatch, 3 for birds that produced nestlings that did not fledge, and 4 for birds that produced a fledgling (successful reproduction), starting with the first year present as a banded adult. Birds not encountered during the annual resighting survey were coded 0. We used Program MARK (White and Burnham 1999) to fit multistate models to this multistate encounter history input file of 2039 cases (Appendix A gives the breakdown of the encounter histories by breeding season, state, and sex) and generate maximum-likelihood estimates of relevant demographic parameters. In Program MARK, we used Parameter Index Matrices and the logit link function for model construction.

A set of candidate models was developed to evaluate state- and sex-specific effects on reproduction and survival. The parameters of interest were survival and transitions between states. Effects of sex, reproductive state, and interactions between these variables were tested. The most reduced (i.e., constrained) model permitted temporal variability in the dependent variables: survival and state transition were permitted to vary with time/age. Encounter probability (p) was a nuisance parameter; we made the simplifying and biologically sound assumption that sex, reproductive state, and temporal variability in the environment would affect the encounter probability. One would reasonably expect a bird in state 1 (egg producer) to have a lower encounter probability, because its presence in the colony may be short, whereas a bird in state 4 (fledgling producer) is considerably more likely to be recaptured/resighted (it must have a long presence in the colony).

Table 1. Candidate models for testing hypotheses on the cost of reproduction and sex-specificity of survival, reproduction, and reproductive costs. In the models, the effects of reproductive state (*r*), sex (*g*), temporal variability (*t*), and interactions (\times) on survival probability (*S*), encounter probability (*p*), and transition probability (ψ) were considered. Note: model selection procedures were used to determine state- and sex-specific effects on survival and fecundity; parameter estimates were used to determine if effects were positive (benefits) or negative (costs).

Model reference	Model	State-specificity		Sex-specificity	
		Survival	Fecundity	Survival	Fecundity
A	$S(r \times g \times t) p(r \times g \times t) \psi(r \times g \times t)$	X	X	X	X
B	$S(r \times g \times t) p(r \times g \times t) \psi(r \times t)$	X	X	X	
C	$S(r \times t) p(r \times g \times t) \psi(r \times g \times t)$	X	X		X
D	$S(r \times t) p(r \times g \times t) \psi(r \times t)$	X	X		
E	$S(g \times t) p(r \times g \times t) \psi(g \times t)$			X	X
F	$S(g \times t) p(r \times g \times t) \psi(t)$			X	
G	$S(t) p(r \times g \times t) \psi(g \times t)$				X
H	$S(t) p(r \times g \times t) \psi(t)$				

For model selection, an information-theoretic approach based on a conservative variant of AIC (QAICc) was used (Burnham and Anderson 2002). The QAICc incorporates a correction factor to adjust for “small” sample size; that is to say, the sample size was small with respect to the number of parameters being estimated. It also incorporates a quasi-likelihood adjustment (a variance inflation factor, \hat{c}) to account for overdispersed data.

CANDIDATE MODELS AND HYPOTHESES TESTED

Table 1 lists the candidate models, following the notation of Lebreton et al. (1992) and Nichols et al. (1994). In the models, the effects of reproductive state (*r*), sex (*g*), temporal variability (*t*), and interactions (\times) with survival probability (*S*) and transition probability (ψ) were considered. Encounter probability (*p*) was also unconstrained. Model A was the global model in which parameters differ for all sources of variability (no parameters were constrained). Models A–D tested sex and state effects on survival and fecundity. Models A–C tested sex-specific effects of reproduction that would support the hypothesis that a male-biased sex ratio is attributable to sex differences in parental investment. Models E–G tested sex-specificity in fecundity and survival that may cause the sex ratio bias, but do not specifically implicate reproductive costs or sex-specific differences in parental investment. Model H was a pseudo-null model, in which none of the effects of interest was modeled; however, survival and state transition probabilities were allowed to vary with time.

Hypothesis testing was a two-stage procedure: (1) determining if a model that included sex- and state-specific effects on survival and fecundity was supported, and (2) determining if state effects were positive or negative by using “real parameter estimates” for survival and state transition probabilities calculated by Program MARK. Model selection procedures were used to de-

termine state- and sex-specific effects on survival and fecundity; real parameter estimates were used to determine if effects were positive (benefits) or negative (costs).

GOODNESS-OF-FIT (GOF) TESTING

Assumptions of these multistate models include: (1) probability of recapture and state transition was the same for all marked animals in the population at time *i* within a given current state *s* and a previous state *r*; (2) survival probability for all subjects in a given state was independent of the others and equal; (3) marks were not lost or missed; and (4) sampling interval was short relative to the time between sampling occasions.

In general, when using the information-theoretic approach, one must first examine the overall fit of the global model to determine if it provides an appropriate umbrella structure from which to start model selection. Program U-CARE (Choquet 2005) has been developed for GOF testing of multistate models. A GOF test for the global model (Table 2, Model D) showed that the data for our global model differed significantly from what would be expected with a standard JMV model (Jolly MoVe, Brownie et al. 1993; $\chi^2 = 877.45, P < 0.001, df = 245$). We attributed the lack of fit to overdispersion and calculated a variance inflation factor, $\hat{c} = 3.58$, 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). Appendix B provides a detailed description of test results.

Assumptions 3 and 4 were reasonably satisfied. Band retention is high (0.982–1.000; Huyvaert and Anderson 2004). The sampling interval for band resighting lasted one to two weeks whereas sampling occasions were annual; thus, the sampling interval was short relative to frequency of sampling occasions.

Table 2. Model selection for mark–recapture models. In the models, the effects of reproductive state (*r*), sex (*g*), temporal variability (*t*), and interactions (*×*) on survival probability (*S*), encounter probability (*p*), and transition probability (*ψ*) were considered.

Model reference	Model	QAICc	ΔQAICc	QAICc weight	Model likelihood	Number of parameters
D	$S(r \times t) p(r \times g \times t) \psi(r \times t)$	8880.1072	0	1	1	168
C	$S(r \times t) p(r \times g \times t) \psi(r \times g \times t)$	8995.1261	115.0189	0	0	252
A	$S(r \times g \times t) p(r \times g \times t) \psi(r \times g \times t)$	9048.6493	168.5421	0	0	280
B	$S(r \times g \times t) p(r \times g \times t) \psi(r \times t)$	9057.4882	177.3810	0	0	196
H	$S(t) p(r \times g \times t) \psi(t)$	9619.8005	739.6933	0	0	70
F	$S(g \times t) p(r \times g \times t) \psi(t)$	9697.6509	817.5437	0	0	77
G	$S(t) p(r \times g \times t) \psi(g \times t)$	9710.7091	830.6019	0	0	77
E	$S(g \times t) p(r \times g \times t) \psi(g \times t)$	9879.0598	998.9526	0	0	84

ADULT SEX RATIO (ASR)

ASR (Wilson and Hardy 2002) was estimated as the proportion of adults in the study colony, during the early part of the breeding season, that were male. In a representative section of our study site, we placed numbered plastic bands on all adults in the section, and noted the presence/absence of each bird each night, the time of day of highest colony attendance, beginning in October 2001. Anytime an unbanded bird was seen in the section at night, it was banded. This comprehensive banding and nightly band re-sight survey (“2001 nightly BRS”) showed which birds were in attendance at different times of year. We used data from November 2001, during the peak of egg laying (which corresponds to the time period when the “annual BRS” is conducted), to estimate the ASR, and closed population mark–recapture models in program Capture (White et al. 1978; Rexstad and Burnham 1991) to determine differences in encounter probability for males and females. Sex-specific differences in nightly recapture probabilities were used to correct population counts and the ASR (eq. 1, as suggested by W. Kendall, pers. comm.)

$$ASR = \frac{\hat{N}_m}{\hat{N}_f + \hat{N}_m} = \frac{n_m / \hat{p}_m}{n_m / \hat{p}_m + n_f / \hat{p}_f}, \quad (1)$$

where \hat{N} denotes population size estimates, n is sample size, \hat{p} is the probability of encounter, and subscripts f and m correspond to female and male, respectively.

Annual trends in ASR from 1984–1985 to 2002–2003 breeding seasons were also examined. The annual ASR trends were calculated from raw counts of males and females in the annual BRS. Any appreciable differences in p_m and p_f , described above, were applied to the raw counts from the annual BRS using equation 1 to account for sex-specific differences in detection probability. The 95% confidence interval for the proportion of males in the annual trends analysis was estimated using a normal approximation to the binomial distribution with a correction for continuity applied (Fleiss 1981). The equation for the margin of error, e , is

listed below (eq. 2); this error is subtracted from and added to the different proportions to calculate a confidence limit.

$$e = z \times \frac{S}{\sqrt{n}}, \quad (2)$$

where $z = 1.96$ for the 95% confidence level, and S is calculated by using equation 3.

$$S = \sqrt{p(1-p)} \sqrt{\frac{(N-n)}{(N-1)}}. \quad (3)$$

Results

MODEL ANALYSIS

The top model among the candidate models is that with the smallest QAIC_c value (i.e., the model in the candidate set using the fewest parameters to adequately describe the variability in the data). In this case, that model (Model D) included reproductive state as a factor influencing adult survival and probability of transition between reproductive states, with no sex-specific effects (Table 2). Model D had a QAIC_c weight of 1.0, indicating that no other model had any meaningful support in the data (Burnham and Anderson 2002). These results indicated an association between current reproductive effort and future survival and reproduction, which did not differ by sex; real parameter estimates (i.e., estimates of the survival and fecundity parameters, rather than the linear model coefficient) were required in the second stage of the procedure to specify the nature of the association.

REAL PARAMETER ESTIMATES

Parameter estimates using Model D indicated that birds that attempted to reproduce (states 2 and 3) or reproduced successfully (state 4) in the 1992–1993 through 1994–1995 breeding seasons had similar annual survival rates, and all had lower survival rates during that period than nonbreeders (state 1) did, consistent with

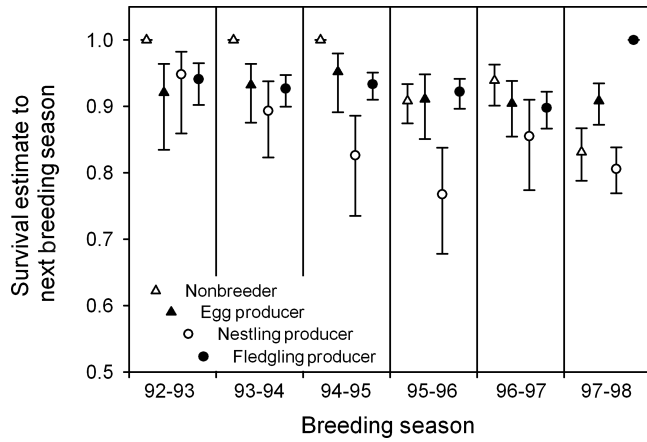


Figure 2. Survival estimates from beginning of breeding season *i* (shown below the corresponding group of four points) to beginning of breeding season *i* + 1 from the top model (Model D in Table 2). Error bars represent 95% confidence intervals. Survival estimates for 1998–1999 are confounded with the final encounter probability (Burnham and Anderson 1999) and are not shown.

the cost of reproduction hypothesis. This association was not evident during the 1995–1996 and 1996–1997 breeding seasons (Fig. 2). During the 1997–1998 ENSO season, birds that produced a fledgling survived at a higher rate, not the lower rate predicted by the cost of reproduction hypothesis, than did those with failed or no reproductive attempts.

In all breeding seasons, nonbreeding birds strongly tended to remain nonbreeders in subsequent years (Fig. 3A). Birds that bred (states 2–4) in the first three breeding seasons all tended to breed successfully in the following year, and with similar transition probabilities (approximately 0.5; Fig. 3B–D). The adverse conditions of the 1997–1998 ENSO event homogenized the success of these breeding birds: virtually all attempted to breed but failed (attained state 3 following the 1996–1997 season), regardless of their reproductive state in 1996–1997. The last two breeding seasons were also characterized by high breeding failure, and most breeders (states 2–4) in 1997–1998 and 1998–1999 changed to nonbreeders or egg producers in the next year (Fig. 3B–D). Notable exceptions to these generalizations involve state 4 birds.

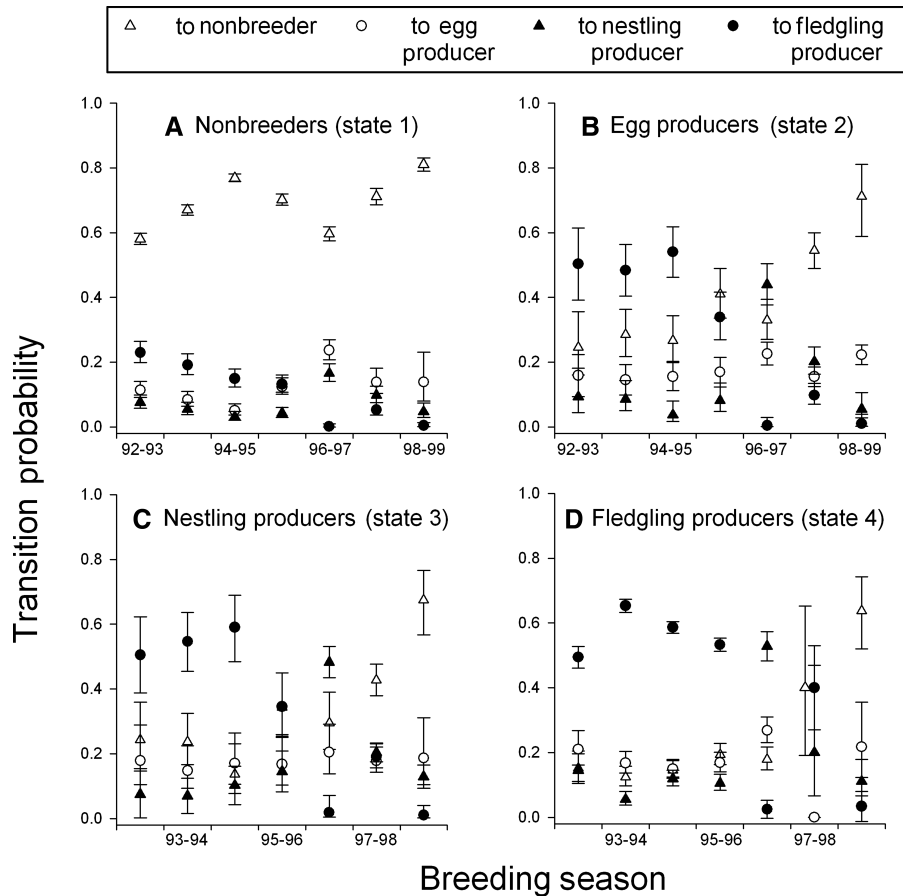


Figure 3. Transition probability estimates for all reproductive states derived from Model D (Table 2). Error bars represent 95% confidence intervals. The probability of remaining in a given reproductive state is derived by subtracting the other transition probabilities from 1 and the 95% error bars were calculated based on a method in Hestbeck et al. (1991).

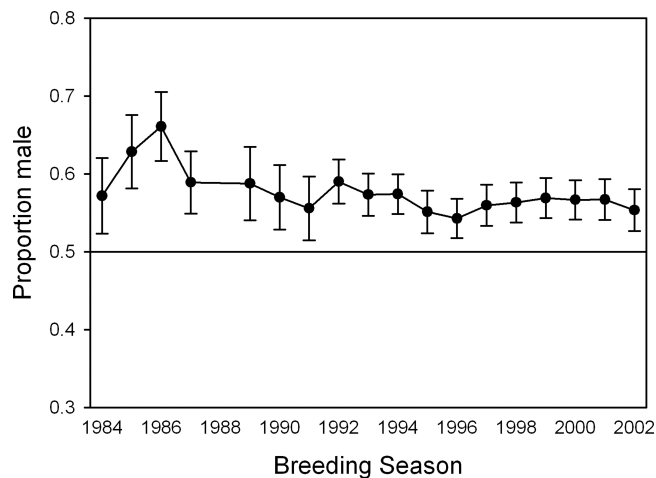


Figure 4. Adult sex ratio (proportion of males) of banded Nazca boobies from 1984 to 2002. Error bars represent 95% confidence intervals. Adult sex ratio is based on raw population counts, not equation 1, because estimates of sex-specific encounter probability do not differ appreciably.

Birds that produced a fledgling in 1995–1996 produced a fledgling in the next season at a higher rate (not a lower rate, as predicted by the cost of reproduction hypothesis) than did birds in states 2 and 3 in 1995–1996 (0.53 vs. 0.34 and 0.35, respectively; Fig. 3). Similarly, the few birds that produced a fledgling during the challenging conditions of the 1997–1998 ENSO event had a higher probability of producing a fledgling in the next year (0.40) than did birds in states 2 and 3 in 1997–1998 (0.10 and 0.19; Fig. 3).

Encounter probability estimates are included in Appendix C. In general, the encounter probabilities were at or near 1 for all reproductive states except nonbreeders. Encounter probability for nonbreeders varied from 0.17 to 0.91.

ADULT SEX RATIO

The ASR of the subset of adults in the nightly BRS in 2001 was male-biased (0.589; 95% CI = 0.589–0.589), and the estimates of sex-specific encounter probability did not differ appreciably ($p_m = 0.85$, 95% CI = 0.82–0.90; $p_f = 0.82$, 95% CI = 0.76–0.87).

The annual estimates of ASR of all banded birds were all male-biased (Fig. 4), and the 95% confidence intervals of most points (in particular, that for the 2001–2002 breeding season) included 0.589.

Discussion

The annual survival probability estimates from the top model of the data provided phenotypic evidence of trade-offs between current reproduction and future survival in Nazca boobies in some years but not in others. When a trade-off was indicated, it was between initiating breeding and survival: nonbreeders had higher

survival than breeders did, but breeders reaching advanced breeding states did not show lower survival than did those failing early. If the energetic costs of producing and raising offspring were the only major factors influencing survival, then we would expect a gradual decrease in survival across breeding states—a simple monotonic response. However, successful and unsuccessful breeders had similar survival probabilities, leading us to consider other factors influencing survival, such as parental quality.

Both survival and reproductive state transition estimates from the top model suggested differences in intrinsic quality among individuals. These differences may have countered costs of reproduction in most years, obscuring evidence of both costs of reproduction and variation in individual quality. Under the most challenging environmental conditions (an ENSO event), strong evidence of intrinsic quality did emerge: parents fledging an offspring under those conditions also displayed notably higher probabilities of survival and fledging another offspring in the subsequent breeding season, even higher than those of nonbreeders. Thus, extreme environmental events may provide “natural experiments” that enable the segregation of costs of reproduction and parental quality as explanatory factors for state-specific survival.

A male-biased ASR was observed for this monogamous bird with biparental care, as predicted by Trivers’ parental investment hypothesis; however, a reproductive state \times sex interaction effect on survival was not observed in the highest ranked multi-state model, indicating that females did not incur excess survival costs of reproduction related to egg production or foraging effort supporting chicks. In general, sex-specific differences in survival costs of reproduction for Nazca boobies do not appear to contribute to the male bias in sex ratio.

In summary, we observed (1) some evidence for costs of reproduction, (2) some evidence for parental quality masking reproductive costs, and (3) no evidence for sex-specific survival differences or survival costs of reproduction that would explain the male-biased ASR.

SURVIVAL COST OF REPRODUCTION

Life-history theory suggests that the cost of reproduction is ubiquitous. Nonexperimental evidence based on phenotypic trade-offs is not definitive, in part, because environmental variability can confound results. Using mark–recapture techniques, we considered variability in survival and reproduction over many years; thus, any temporal changes in the environment that would affect reproductive costs become evident.

The temporal component of our study provided significant insight into the importance of reproductive costs. Until the 1994–1995 breeding season, nonbreeding birds (state 1) had a higher survival rate than did birds that attempted to breed (states 2 and 3) or bred successfully (state 4; Fig. 2); this result provides evidence for a survival cost of reproduction (specifically, of initiating

breeding) during those years. This effect was not observed after the 1994–1995 breeding season, and in fact, an opposite result was observed following the challenging conditions of the 1997–1998 ENSO event (Fig. 1): parents fledging a chick during that season actually had markedly higher survival to the next breeding season, even compared to nonbreeders. This evidence of a positive correlation of reproductive success and survival emerged only under adverse conditions, but we suspect that variation in overall performance affected all of our results concerning adult survival. In no year did those birds attempting to breed (states 2–4) show a negative correlation between breeding state attained and subsequent survival (the 95% CIs for each survival estimate in Fig. 2 are particularly useful in this case), as predicted by the cost of reproduction hypothesis. Yet, evidence of a survival cost of reproduction existed in the comparison of breeders and nonbreeders.

We attribute the apparent discordance of these results to the opposing effects of costs of reproduction and individual quality on survival, and we suggest the following explanation: (1) survival costs of reproduction rise with increasing parental effort; (2) higher-quality individuals are more likely to breed than are low-quality individuals, and thus to incur those survival costs; (3) among birds attempting to breed, the positive effect of individual quality on survival approximately offsets the negative effect of parental investment: higher-quality individuals reach advanced stages of breeding more often—they also enjoy higher intrinsic ability to survive. Under this hypothesis, the survival cost of initiating breeding has a higher magnitude in some years than does the cost of continuing breeding or the countervailing benefit of high individual quality, accounting for the relatively high survival of nonbreeders in some years. This survival cost of initiating breeding probably does not involve the cost of egg production, because we detected no sex difference in survival rates, and we detected no survival cost of egg production to females in a related study (H. Townsend and D. J. Anderson, unpubl. ms.). Instead, it may involve density-dependent or other effects resulting from presence in the colony and in nearby feeding areas.

The indication that costs of reproduction have a magnitude that is sometimes similar to the difference in intrinsic survival ability between classes of breeders is a notable result. These two opposing demographic factors may be likely to approximately balance each other in long-lived organisms like pelagic seabirds, whose life history includes a low ceiling on reproductive effort (Goodman 1974), wide variation between individuals in breeding performance (Moreno 2003), and positive correlations between survival and breeding probabilities (Cam et al. 2002). Shorter-lived species may instead tolerate higher costs of reproduction that generally swamp any countervailing effects of intrinsic quality on future performance.

FECDITY COST OF REPRODUCTION

Our data provided no evidence of a fecundity cost of reproduction. Parents producing a fledgling were not less likely to produce a fledgling in the following breeding season compared to parents reaching a lower breeding state (Fig. 3). They were not more likely to attain a lower breeding state in the following season than were less successful breeders, either (and the reverse was true in some seasons; Fig. 3). As was the case with survival, parents that produced a fledgling during the 1997–1998 ENSO event were markedly more likely to produce a fledgling in the following breeding season than were birds in other reproductive states (compare the filled circles and 95% CIs for the 1997–1998 season in Fig. 3A–D), providing further evidence of the effect of individual quality on demographic life histories. As with survival, we do not conclude that fecundity costs of reproduction were absent during this study, but rather that evidence of the costs is masked by correlated variation in individual quality.

As is generally the case, experimental manipulation of families should help to elucidate the role of costs of reproduction in the evolution of Nazca biology reproduction. Nur (1990) recommended the use of experimental studies to measure reproductive costs in the wild to account for differences in parental quality. Similarly, Nichols et al. (1994) cautioned that the multistate mark–recapture technique for measuring reproductive costs can be used primarily for detecting costs of reproduction based on phenotypic correlations, and are helpfully complemented by other studies that measure or control genotypic correlations. The strength of the multistate mark–recapture technique is its ability to accurately account for multiple sources of variability (e.g., encounter probability) that may confound accurate assessment of phenotypic correlations between current reproduction and survival as well as current reproduction and near-term future reproduction. In the case of this study, it also facilitated a long-term study that would be logistically difficult in an experimental mode. The value of a long-term approach is evident from the temporal heterogeneity in our results: had the study not included the first three breeding seasons, no evidence for a survival cost of reproduction would have been detected. Had the study not included the ENSO event, no compelling evidence for a parental quality effect on fecundity would have been detected.

SEX RATIO BIAS AND PARENTAL INVESTMENT

No sex-specific effects or reproductive state \times sex interaction effects on survival and fecundity were evident in this analysis. Although a male-biased sex ratio is apparent (Fig. 4), the mark–recapture analysis did not support the cost of reproduction hypothesis to explain the male-biased sex ratio in this monogamous seabird. Other work suggests that the male-bias arises during the subadult period of several years spent away from the colony and

the “return sex ratio” measured at the first appearance as an adult averages 0.575 (Maness et al. 2007), similar to our estimate for the ASR of 0.589.

The central tenet of this hypothesis is that egg production and other reproductive effort made in excess by females contributes to higher female mortality. In this analysis, the key model that would have supported this hypothesis included a state by sex interaction in the survival parameter, model A or B in Table 1. Moreover, the survival of females in state 2 would have been lower than males in state 2. This analysis is a conservative test of this tenet. Females that had eggs developing but never laid would have been classified in state 1 (nonbreeders), even though the physiological cost of egg production had been incurred, because costs of egg production could not be observed in cases in which an egg was not observed. In addition, this test assumes that costs of parental care aside from egg production are negligible for Nazca boobies relative to costs of egg production, or that other sex-specific parental effort does not mask the cost of egg production.

Liker and Székely (2005) reviewed and synthesized research on sex-specific differences in cost of reproduction and pointed out that in avian reproductive systems, sex-specific mortality bias increases with sex-specific biases in parental care and mating competition. Nazca boobies seem to show sex differences in parental care, with females laying eggs, delivering larger loads of food to the nest (Anderson and Ricklefs 1992), spending more time foraging during the nestling period (V. Apanius, M.A. Westbrook, and D.J. Anderson, unpubl. ms.), and breeding more frequently than males do because the sex ratio is male-biased (Maness et al. 2007). However, we lack analyses of effort by males in mate competition or defense of territory prior breeding, which could impose significant costs. During the nonbreeding season, males attend the colony more than females do, apparently maintaining possession of nesting sites (D.J. Anderson, unpubl. data); females are thus free to vacate the colony and may move to distant habitats to recover condition following breeding. Thus, male effort spent in territory defense may offset female effort in parental care, thereby balancing sex-specific reproductive costs.

Other models that included sex-specific effects were tested, Models C, E, F, and G (Table 1), although none were supported. Age \times sex interactions were not tested in the information-theoretic model-selection process used in our methods because of insufficient age-specific data, but other work on this species detected no difference in age-specific adult mortality rates for the two sexes (Anderson and Apanius 2003). Furthermore, in considering sex ratio by banding cohort, which is roughly correlated with age, the sex ratio was male-biased in the majority of cohorts during most of the breeding seasons (Townsend 2004), implying that the male-biased sex ratio was not explained by sex-specific differences in adult survival.

Although we are able to offer an ad hoc explanation of the apparent lack of sex-specific reproductive costs, an explanation of the male-bias in sex ratio of Nazca boobies is elusive. Undetectable sex-biased mortality in adult Nazca boobies is a potential, but unsatisfactory, explanation. Thorough research on sex-biased mortality at other life-history stages of this study species would likely be more fruitful.

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APPENDIX A

Table A1. Summary of encounter histories by year, reproductive state (see Materials and Methods), and sex used for cost of reproduction analysis.

Breeding season	State	# Females	#Males
1992–1993	0	524	487
	1	265	367
	2	39	43
	3	36	35
	4	119	124
1993–1994	0	477	431
	1	131	199
	2	66	96
	3	62	67
1994–1995	4	247	263
	0	380	343
	1	130	179
	2	75	94
1995–1996	3	49	58
	4	349	382
	0	434	416
	1	103	156
1996–1997	2	88	87
	3	58	60
	4	300	337
	0	329	309
1997–1998	1	171	304
	2	137	122
	3	65	62
	4	281	259
1998–1999	0	388	356
	1	84	278
	2	204	178
	3	298	236
1999–2000	4	9	8
	0	412	439
	1	275	365
	2	102	83
1999–2000	3	115	98
	4	79	71
	0	412	447
	1	408	496
1999–2000	2	108	86
	3	46	24
	4	9	3

APPENDIX B

In general, the U-CARE tests are used to ascertain the structural integrity of the model and to test the assumptions of the independence of individuals, which is required by the multinomial distribution that underlies this type of model. First a general, overall

GOF test (composed of several smaller tests) is conducted. If the overall GOF test is not significant, then one can assume sufficiency of the model structure. Alternatively, if the null hypothesis of the overall test is rejected, then further exploration of the model structure, by examining the subtests of which the overall test is composed, is required.

For this work, the overall test was found to be significant, which led us to further investigation, to ensure that we were not violating the assumptions of the JMV models. The major overarching assumption is that all animals present at any given time in the same state behave the same. According to Pradel et al. (2005) this can be verified by checking “two (conditionally) independent points: (1) animals released together have the same expected future whatever their past encounter history and (2) animals present at the same site at the same date that are eventually reencountered do not differ in the timing of their reencounters whether they are currently encountered or not. Thus, apart from the precision of a common site [state], the exact same two main components are retrieved.”

We examined the component tests for the overall JMV GOF tests and individual subcomponent GOF tests (i.e., observed vs. expected frequencies for each for each recapture-occasion \times state cell) and found no clear pattern of a particular insurance state or time period that invalidated the overarching assumptions of JMV models for multistate model; details of the component tests are provided below. Thus, we decided that the lack of fit to the model was due to overdispersion, rather than structural failure of the model. In this case, a correction factor \hat{c} was calculated.

Test WBWA (where before, where after)

The null hypothesis of no difference in the expected state of next reencounter among the individuals previously encountered in the different state was rejected (Group 1: $\chi^2 = 165.2$, $P < 0.001$, $df = 108$ and Group 2: $\chi^2 = 165.9$, $P < 0.001$, $df = 100$). For most of the observed versus expected frequencies for each recapture-occasion \times state cell, the null hypothesis was not rejected. There was no discernible pattern of cells in which the null hypothesis was rejected.

Test 3G.SR

The null hypothesis that there is no difference in the probability of being later reencountered between the newly marked individuals and individuals marked at earlier times was not rejected ($\chi^2 = 20.9$, $P = 0.139$, $df = 15$).

Test 3G.Sm

The null hypothesis of no difference in the expected time at first reencounter between the individuals encountered at occasion I in state l that have been encountered earlier and will be next reencountered in state j based on their state of most recent encounter

was rejected (Group 1: $\chi^2 = 361.2, P < 0.001, df = 104$ and Group 2: $\chi^2 = 285.14, P < 0.001, df = 116$). For most of the cells, the null hypothesis was not rejected. There was no discernible pattern of cells in which the null hypothesis was rejected.

Test M.ITEC (immediate trap effect on capture)

The null hypothesis of no difference in the probabilities of being reencountered in different states between the animals encountered and not encountered at the previous occasion then in the same state, conditional on presence at both occasions was rejected (Group 1: $\chi^2 = 415.2, P < 0.001, G = 463.0, P < 0.001, df = 7$ and Group 2: $\chi^2 = 394.4, P < 0.001, G = 414.2, P < 0.001, df = 11$). Further inspection of reencounter tables generated by U-CARE for the

M.ITEC did not provide evidence of a clear pattern of immediate trap dependence for a given state.

TEST M.LTEC (long-term trap effect on capture)

The null hypothesis that there is no difference in the expected time and state of next reencounter between the individuals in the same state at occasion i that were not encountered at occasion $i + 1$ whether encountered or not encountered at occasion i conditional on presence at both occasions i and $i + 2$ was rejected (Group 1: $\chi^2 = 13.45, P = 0.004, G = 8.30, P = 0.04, df = 3$ and Group 2: $\chi^2 = 11.14, P = 0.011, G = 10.30, P = 0.016, df = 3$). Further inspection of reencounter tables generated by U-CARE for the M.LTEC did not reveal a discernible pattern of long-term trap dependence for a given state.

APPENDIX C

Table A2. Encounter rate estimates by year and reproductive state for male and female Nazca boobies.

Male					Female		
State	Breeding season	Encounter rate estimate	95% Lower CL	95% Upper CL	Encounter rate estimate	95% Lower CL	95% Upper CL
Nonbreeder	1992–1993	0.547	0.485	0.608	0.322	0.259	0.393
	1993–1994	0.446	0.388	0.506	0.219	0.171	0.277
	1994–1995	0.378	0.328	0.431	0.172	0.133	0.218
	1995–1996	0.632	0.580	0.680	0.402	0.346	0.461
	1996–1997	0.733	0.681	0.778	0.325	0.268	0.386
	1997–1998	0.891	0.813	0.939	0.793	0.743	0.835
Egg producer	1992–1993	1.000	1.000	1.000	1.000	1.000	1.000
	1993–1994	1.000	1.000	1.000	1.000	1.000	1.000
	1994–1995	1.000	1.000	1.000	1.000	1.000	1.000
	1995–1996	1.000	1.000	1.000	1.000	1.000	1.000
	1996–1997	1.000	1.000	1.000	1.000	1.000	1.000
	1997–1998	0.800	0.531	0.934	1.000	1.000	1.000
Nestling producer	1992–1993	0.834	0.113	0.995	0.998	0.000	1.000
	1993–1994	1.000	1.000	1.000	1.000	1.000	1.000
	1994–1995	1.000	1.000	1.000	1.000	1.000	1.000
	1995–1996	1.000	1.000	1.000	1.000	1.000	1.000
	1996–1997	1.000	1.000	1.000	1.000	1.000	1.000
	1997–1998	1.000	1.000	1.000	1.000	1.000	1.000
Fledgling producer	1992–1993	0.603	0.309	0.837	1.000	1.000	1.000
	1993–1994	1.000	1.000	1.000	1.000	1.000	1.000
	1994–1995	1.000	1.000	1.000	1.000	1.000	1.000
	1995–1996	1.000	1.000	1.000	1.000	1.000	1.000
	1996–1997	1.000	1.000	1.000	1.000	1.000	1.000
	1997–1998	1.000	1.000	1.000	1.000	1.000	1.000
Fledgling producer	1992–1993	1.000	1.000	1.000	1.000	1.000	1.000
	1993–1994	1.000	1.000	1.000	1.000	1.000	1.000
	1994–1995	1.000	1.000	1.000	1.000	1.000	1.000
	1995–1996	1.000	1.000	1.000	1.000	1.000	1.000
	1996–1997	1.000	1.000	1.000	1.000	1.000	1.000
	1997–1998	1.000	1.000	1.000	1.000	1.000	1.000