

# Food limitation explains most clutch size variation in the Nazca booby

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## Summary

1. Natural selection is expected to optimize clutch size, but intrapopulation variation is maintained in many bird species. The Nazca booby provides a simple system in which to investigate clutch size evolution because clutch size and brood size are decoupled due to obligate siblicide. The indirect effect of brood size on clutch size evolution can therefore be eliminated.

2. In Nazca boobies, second eggs provide insurance against the failure of the first egg or early death of the first hatchling, but approximately half of all females lay only one egg. We tested the hypothesis that one-egg clutches result from food limitation by providing female Nazca boobies with supplemental food.

3. A higher proportion of supplemented females produced two-egg clutches than did control females. Supplemented females produced larger second-laid eggs than did control females, but not first-laid eggs. Laying date and laying interval were not affected.

4. Comparisons of clutch size and egg volume between years indicated that the supplemental feeding experiment was not conducted in a year with a poor natural food supply. Thus supplemented females produced larger clutch sizes despite apparently normal natural food levels.

5. This experiment nearly completes our understanding of clutch size variation in the Nazca booby, and indicates that food limitation and the costs of egg-laying should be considered carefully in studies of clutch size evolution.

*Key-words:* egg production, egg size, nutrient availability, *Sula granti*, supplemental feeding.

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## Introduction

A wide range of clutch size variation exists among bird species. For example, albatrosses of the genus *Diomedea* produce an invariant clutch size of one egg (Warham 1990), tree swallows (*Tachycineta bicolor*) produce an intermediately variable clutch of 4–6 eggs (Ehrlich, Dobkin & Wheye 1988), and great tits (*Parus major*) produce a highly variable clutch size of 1–17 eggs (Boyce & Perrins 1987). Natural selection is expected to optimize clutch size in a given population, so the maintenance of variation within a population requires explanation.

In no case has a model system provided a comprehensive understanding of observed phenotypic variation in clutch size. Since a variety of factors could influence clutch size, a simplified system is desirable if we wish to

gain such an understanding. Some bird species exhibit variation in clutch size, but their obligate siblicide produces a fixed brood size of one (Mock & Parker 1997). These species provide a simple model system in which clutch size variation can be analysed in the absence of brood size variation. David Lack hypothesized that clutch size in altricial birds is limited by the brood size that parents can feed (Lack 1947; Lack 1954), and studies of avian clutch size evolution have centred on this indirect brood-size effect. In obligately siblicidal birds, this selective factor is minimized, and evolution of clutch size *per se* can be evaluated directly.

Nazca boobies (*Sula granti*) are obligately siblicidal seabirds breeding on oceanic islands in the eastern Pacific ocean. They lay one- or two-egg clutches, with the proportion of two-egg clutches in the population varying between years (Anderson 1990). Incubation begins with the laying of the first egg, resulting in a hatching asynchrony of 3–10 days (Anderson 1989b). If both eggs in a two-egg clutch hatch, the first-hatched chick

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invariably pushes its sibling from the nest scrape, causing its death through exposure or predation (Anderson 1993). Nazca boobies provide a simple system in which to examine clutch size, in which clutch size varies but brood size does not.

Experimental and nonexperimental evidence from Nazca boobies indicates that second eggs in two-egg clutches often provide a nestling if the first egg fails, or if the first chick dies shortly after hatching (Anderson 1990; Clifford & Anderson 2001). Parents provided with an 'insurance' egg shortly after laying have higher reproductive success than do parents with one-egg clutches (Clifford & Anderson 2001). Nazca boobies apparently never produce three-egg clutches (Nelson 1978; Anderson 1993), and a cost-benefit analysis showed that the cost of producing a third egg would outweigh its marginal additional insurance benefit (Anderson 1990). Stabilizing selection appears to favour two-egg clutches; however, the experiment demonstrating the insurance value of second eggs did not incorporate the cost of laying that egg (the egg was provided from another clutch; Clifford & Anderson 2001). Clutch size variation between individuals may reflect an adaptive response to a particular individual's condition (Drent & Daan 1980; Högstedt 1980) such that for some parents experiencing food limitation, the cost of egg production and incubation may exceed the insurance benefit.

If we understood why some individuals produce single-egg clutches despite the apparent advantage of two-egg clutches, we would have a comprehensive understanding of this model system. We propose that single-egg clutches are produced by female Nazca boobies under food limitation, and we test this hypothesis by providing supplemental food to prebreeding females. Most supplemental feeding experiments cannot discriminate the possibility that increases in clutch size result (1) from a release from nutrient limitation, or (2) from anticipation of the ability to feed a larger brood. The obligately siblicidal nature of this species allows the examination of nutrient limitation in isolation from potential increases in brood size.

The Nazca boobies of the Galápagos have traditionally been considered masked boobies (*Sula dactylatra*), but recent analyses of morphological and breeding data (Pitman & Jehl 1998), and of mtDNA differentiation (V. L. Friesen *et al.*, unpublished) support elevation of the Galápagos and nearby populations to species status. In this paper we follow the nomenclature of Pitman & Jehl (1998) and the American Ornithologists' Union (2000), and refer to these birds as Nazca boobies.

## Methods

This experiment was conducted at the large breeding colony at Punta Cevallos, Isla Española, in the Galápagos Islands (1°20'S, 89°40'W; see Anderson & Ricklefs 1987) during the 1997–98 breeding season (October–June). The colony was searched for paired Nazca boobies that did not have any eggs; allopreening and standing together at nest sites were considered signs of pairing. One hundred and eight pairs of Nazca boobies were identified and colour-banded, and then randomly assigned to experimental or control groups. Each pair's nest site was marked with numbered flagging tape. Colour-banded birds did not reappear at five of the nest sites, leaving a total of 103 pairs (50 experimental and 53 control). Females in the experimental group were provided with mullet (*Mugil cephalus*) twice daily; mullet were fresh-frozen, then thawed to ambient temperature before feeding. The normal diet of Nazca boobies comprises primarily sardines (*Sardinops sagax*; Anderson 1993), which are similar in gross composition to mullet (Table 1). Adults readily accepted fish that were weighed, then tossed to them; entire fish were swallowed whole. In the evening (16:00–18:30 h), females were provided fish *ad libitum*. In the mornings (05:30–08:00 h), females were provided with no more than 200 g of fish, if they had been present at their nest site the night before, to minimize disruption of their motivation to forage normally. However, if a female had not been at her nest site the night before, and therefore received no supplemental food, she was provided with fish *ad libitum* in the morning.

The relationship between field metabolic rate (FMR) and body size for seabirds using flapping flight is described by the equation  $\log y = 3.19 + 0.726 \log x$ , where  $y = \text{FMR in kJ day}^{-1}$  and  $x = \text{mass of bird in kg}$  (Birt-Friesen *et al.* 1989). Female Nazca boobies have an average mass of 1.9 kg (Nelson 1978), resulting in an estimated FMR of 2450 kJ day<sup>-1</sup>. Fish provide approximately 3.97 kJ g<sup>-1</sup> (Croxall, Prince & Ricketts 1985). Therefore, females should need approximately 617 g day<sup>-1</sup> of fish to satisfy energetic requirements. The fish provided to them in the morning therefore represented no more than 1/3 of their daily requirement.

Nazca boobies lay one or two eggs at an interval of 4–9 days (Anderson 1993). Therefore, females were supplemented until 10 days had passed without a new egg being laid. Females in the control group were approached twice daily just as the supplemented females were, but were only shown fish. Males were not provided with supplemental food. All nests were monitored daily until the end of the nesting attempt, and egg length and

**Table 1.** Gross composition of natural prey items found in Nazca booby diet and fish provided as supplemental food. Values are percentages of total composition

	Lipid	Protein	Ash	Moisture	Source
<i>Sardinops sagax</i>	2.09–15.34	17.22–18.98	3.25–5.78	63.83–75.07	David DePue, personal communication
<i>Mugil cephalus</i>	10.7	19.5	5.5	64.4	Vlieg (1984)

breadth was measured to the nearest 0.1 mm with vernier calipers. First-laid eggs are referred to as 'A-eggs' and second-laid eggs as 'B-eggs'. Chick mass was measured on the day of hatching using a Pesola spring scale.

To determine if supplemental feeding affected female condition, a subset of females (six control females and six supplementally fed females) was weighed with Pesola spring scales on the day of banding, and then again 10–12 days after the experiment had begun. All females were weighed between 02:30 h and 07:30 h; since most foraging by breeders occurs during daylight hours (Anderson & Ricklefs 1987), their digestive tracts were presumably empty and their weight reflected their true body mass. Percentage of change in female mass by group was calculated using these two weighings.

To determine if supplemental feeding occurred during the period of egg formation, each female was fed a gelatin capsule filled with either red or blue lipophilic dye every 3 days in a sequence with no repeating motif (red–red–blue–red–blue–blue–red–red–red). The dye was incorporated into the discrete yolk layer added to the outside of the developing yolk on the day of feeding (Gilbert 1972; Grau 1982), and sequences of at least three coloured rings in the yolk allowed determination of the dates of deposition. Eight B-eggs were collected on the day they were laid, boiled, and sliced in half. The dye pattern present in the yolk was then noted. All eight eggs provided interpretable dye rings.

In addition to augmenting a female's resources directly, supplemental feeding may affect a female's nutritional status indirectly if she decreases her foraging effort and thus decreases her energetic expenditure. To determine if supplemented females altered their daily time budgets, nests were visited seven times a day during daylight hours (05:30, 08:00, 10:00, 12:00, 14:00, 16:00 and 18:30 h) and the presence or absence of the female from the nest site was recorded. Radio-tracking data indicate that breeding Nazca boobies are generally foraging when absent from their nest sites, and they forage principally during daylight hours (Anderson & Ricklefs 1987). It was therefore assumed that when females were not present at their nest site, they were foraging. Females absent for two consecutive nest checks were assumed to be foraging for the entire interval between those nest checks. Females absent for one nest check and present for the next were assumed to be foraging for half of the interval between checks (Anderson & Ricklefs 1992). The time spent foraging by supplemented and control females was compared.

The end of 1997 marked the beginning of an El Niño Southern Oscillation event, which may have affected breeding conditions for Nazca boobies. Clutch size and egg volume were examined for indications that 1997 was an unusual year. The proportion of two-egg clutches laid at a random sample of nests at the Punta Cevallos colony during the period of the experiment (October 22–November 27) was calculated and then compared to the proportion of two-egg clutches laid during the

same period at the same site in six other years (1992–96, 1998). Mean egg volumes during the experiment were also compared to the volumes observed in five other years (1993–96, 1998).

Statistical tests were performed using Statistica 5.5 (StatSoft, Inc. 1999). All tests were two-tailed.

## Results

Two control females obtained some supplementary food by accident, and one female from the supplemented group never took supplemental food. These three females were removed from the analyses, leaving 51 control and 50 supplemented females. Supplemented females received an average of 262.2 g (range 0–1005 g) of supplemental fish on the days that they were found at their nest site. Females received an average total of 5573.3 g (range 587–11 673 g) of fish over the course of the experiment, consuming supplemental food on an average of 17.2 days (range 3–35 d). Seventeen per cent of morning feedings were *ad libitum* because females had been absent from their nest site the evening before. Ten to 12 days after the experiment began, six supplemented females had increased in mass by an average of 194.2 g (range 90–430 g), while six females from the control group had decreased in mass by an average of 35 g (range –225 g to 150 g;  $t = 3.10$ , d.f. = 10,  $P = 0.01$ ).

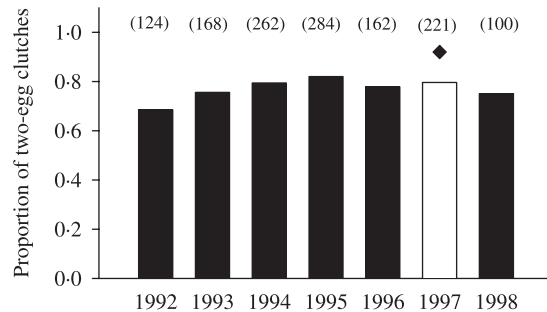
Two females, one from the control group and the other from the supplemented group, never laid eggs. Of 49 supplemented females that laid eggs, 45 (92%) laid two-egg clutches, whereas only 35 of 50 (70%) control females that laid eggs laid two-egg clutches ( $\chi^2 = 7.61$ , d.f. = 1,  $P < 0.01$ ). The proportion of supplemented females laying two-egg clutches was also higher than the proportion of females from a random sample that laid contemporaneous two-egg clutches in the Punta Cevallos colony (0.80;  $\chi^2 = 4.02$ , d.f. = 1,  $P = 0.045$ ). The proportion of control females laying two-egg clutches did not differ from that laid by the random sample of females ( $\chi^2 = 2.20$ , d.f. = 1,  $P = 0.14$ ). The average date of clutch initiation for supplemented females was 1 November, and for control females was 4 November ( $t = 1.35$ , d.f. = 96,  $P = 0.18$ ).

Food-limited females might produce smaller eggs, or lay at shorter intervals, than they would under better food conditions. Females that receive supplemental food may then allocate resources to increase egg size. One control female and one supplemented female laid unexpectedly small B-eggs ( $> 3$  SD from the mean); these two outliers were excluded from the egg volume analysis. Repeated measures ANOVA of egg volumes for two-egg clutches showed a significant effect of laying sequence (A or B;  $F_{1,74} = 132.1$ ,  $P < 0.01$ ) and a significant sequence by treatment interaction ( $F_{1,74} = 4.3$ ,  $P = 0.04$ ). The interaction resulted from larger differences between treatment groups in B-egg size than in A-egg size; contrast analysis showed that supplementally fed females laid significantly larger B-eggs, but not A-eggs, than did control females (Table 2). A-eggs from

**Table 2.** Egg volumes of supplemented and control females laying two eggs. Egg volume calculated as  $0.00051 \times \text{length} \times \text{breadth}^2 + 1.22$  (modified from Anderson 1993). Values represented as  $\bar{x} \pm \text{SD}$  ( $n$ )

	A-egg volume (mm <sup>3</sup> )	B-egg volume (mm <sup>3</sup> )
Supplemented	73.0 ± 5.14 (44)†	68.4 ± 4.89 (44)*
Control	72.3 ± 5.09 (32)†	65.8 ± 6.06 (32)*

† $F_{1,74} = 0.3$ ,  $P = 0.60$ ; \* $F_{1,74} = 4.4$ ,  $P = 0.04$ .



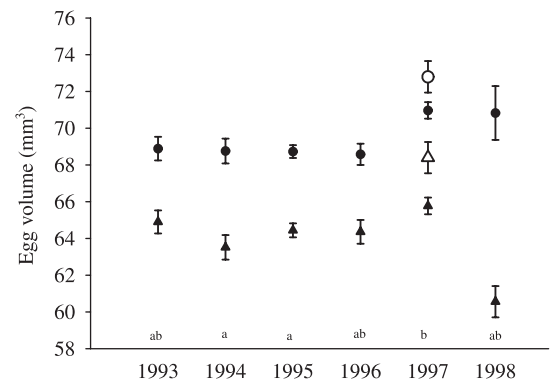
**Fig. 1.** Proportion of clutches initiated between October 22 and November 27 that contained two eggs. These clutches were produced by a subpopulation in a demography study of Nazca boobies at the site where the supplemental feeding experiment was carried out. The proportion of two-egg clutches produced by females receiving supplemental food in the 1997 experiment is represented by the diamond. Sample sizes are in parentheses.

supplementally fed and control females that laid one-egg clutches did not differ in volume (Mann–Whitney  $U = 14.0$ ,  $P = 0.38$ ). B-egg volume was not related to the probability of the B-egg hatching (logistic regression,  $\chi^2 = 1.11$ , d.f. = 1,  $P = 0.29$ ). However, B-egg volume was correlated with B-chick mass ( $R^2 = 0.62$ ,  $F_{1,14} = 25.2$ ,  $P < 0.001$ ). The laying interval between first and second eggs did not differ between supplemented ( $5.4 \pm 1.36$  d) and control ( $5.2 \pm 1.15$  d) females ( $t = 0.825$ , d.f. = 77,  $P = 0.41$ ).

Supplemented females spent less time foraging (4.1 h/day) than control females did (7.7 h/day;  $t = 4.9$ , d.f. = 51,  $P < 0.001$ ) prior to clutch initiation.

Dye patterns in the egg yolk indicated that yolk formation began 18–21 d before the B-egg was laid, and required between 16 and 19 days. On average, females began receiving supplemental food  $8.8 \pm 7.4$  days before laying the A-egg and  $13.9 \pm 7.4$  before laying the B-egg. Sixty-three per cent of the supplemented females began taking supplemental food less than 18 days before the B-egg was laid. Of those females that began B-egg formation after supplemental feeding began, 90% of 18 supplementally fed females produced two-egg clutches while only 59% of 22 control females produced two-egg clutches ( $\chi^2 = 4.41$ , d.f. = 1,  $P = 0.04$ ).

In the random sample of Nazca boobies, the frequency of two-egg clutches in 1997 did not differ from the frequency of two-egg clutches initiated in the same period in six other years at this same site ( $G = 10.56$ , d.f. = 6,  $P > 0.10$ ; Fig. 1). Egg volumes for clutches



**Fig. 2.** Egg volumes of two-egg clutches initiated between October 21 and November 27 by supplemented females and by females in a demography study (see Fig. 1). Values are mean  $\pm$  SE. Years with no letters in common are significantly different ( $P < 0.05$ ). ●, A-eggs from long-term study; ▲, B-eggs from long-term study; ○, experimental A-eggs; △, experimental B-eggs.

initiated during this period in 1997 either did not differ from or were larger than egg volumes for clutches initiated during this period in five other years ( $F_{1,5} = 5.73$ ,  $P < 0.01$ ; Fig. 2).

## Discussion

Two lines of evidence suggest that supplemental food had the potential to influence clutch sizes of female Nazca boobies. First, mass of supplementally fed females increased during the experiment, while that of control females either decreased, or increased to a lesser degree. These results indicate that the supplemental food increased the physiological condition of experimental females compared to that of controls. Secondly, lipophilic dye patterns in egg yolks indicated that supplemental food was provided during the period of egg formation.

Supplemented females produced two-egg clutches more frequently than did control females. Increases in clutch size of supplemented females may result from a release from nutrient limitation on egg formation or incubation, or because supplemental food provides females with cues that more food will be available for raising nestlings (limitation on brood size; Nilsson 1991). Most supplemental feeding experiments can not distinguish these two alternatives. Obligate siblicide allows the latter hypothesis to be ruled out for Nazca boobies. Parents have only a brood of one to raise regardless of clutch size, and therefore information about the amount of food available to provision chicks is not relevant to the optimal clutch size. We can therefore conclude that the clutch size itself of some Nazca boobies is nutrient limited.

We envision two possible forms of nutrient limitation at the egg stage. The first possibility is that a lack of sufficient nutrients or energy constrains a female's ability to produce and lay a second egg. For example, there is evidence that in queleas (*Quelea quelea*), females' energy

reserves are reduced to the level that to lay one more egg would result in death (Jones & Ward 1976). Alternatively, nutrient limitation may cause the cost of producing and laying a second egg to outweigh the benefit so that females practice restraint (Curio 1983; Desrochers 1992) and do not produce the second egg. Under the second scenario, the cost of egg production may be paid during egg formation, chick rearing and/or in the female's future. If costs of egg production affect females during chick rearing, as has been demonstrated in common terns (*Sterna hirundo*; Heaney & Monaghan 1995) and lesser black-backed gulls (*Larus fuscus*; Monaghan, Nager & Houston 1998), then altered information about future food conditions that supplemental food provides is important because it changes the cost : benefit ratio of egg production. Altered information about the future environment may therefore be relevant to clutch size evolution in this species, but the important distinction between this scenario and the above hypothesis (more food available for chick rearing) is that the altered information is applied to balancing costs of egg production and laying, and not the number of young that the parents will rear. Either or both forms of nutrient limitation could be relevant to Nazca boobies.

Most supplemental feeding experiments with birds caused advanced laying dates, but not increased clutch sizes (reviews in Martin 1987; Arcese & Smith 1988; Boutin 1990; Meijer & Drent 1999). It has been suggested that laying date determines clutch size independently of food intake and body condition (Meijer & Drent 1999). However, supplemental food increased clutch size of Nazca booby females without advancing lay date, indicating that clutch size is not mediated strictly through clutch initiation date in this species.

Many experimental females apparently had already begun formation of the B-yolk when they began receiving supplemental food. Since extra food led to the ovulation and laying of these yolks, the effect of the food was to maintain vitellogenesis, not to initiate it. As in gulls (Houston, Jones & Sibly 1983), penguins (Astheimer & Grau 1985) and shags (Grau 1996) more ova apparently undergo yolk enlargement than are laid, and extra ova are reabsorbed through atresia (Gilbert 1979). Therefore, final clutch size may not be determined until near the time of ovulation. The single opportunity that we had to dissect a recently dead female during yolk formation corroborated this suggestion. The female had one partially calcified egg in the oviduct and two enlarged ova with substantial yolk deposition, yet Nazca boobies never produce three-egg clutches (Anderson 1993). Regardless of when clutch size is determined, supplemental food clearly influenced final clutch size, as was indicated by the significantly larger clutch sizes of the subset of females that began receiving supplemental food before B-yolk formation began compared to control females.

The end of 1997 marked the beginning of an El Niño Southern Oscillation event, which typically affects

adversely the normal prey species eaten by Nazca boobies (Anderson 1989a). Measures of natural food availability are not available for Nazca boobies, but a relationship between food and clutch size, and food and egg volume, has been demonstrated in this experiment, and therefore food availability can be inferred from reproductive performance in this species. The proportion of two-egg clutches produced by the random sample of Nazca boobies at the Punta Cevallos colony during the period of the experiment did not differ from the proportion of two-egg clutches produced during this same period in six other years. This indicates that this experiment was not performed during a period of food shortage. Further evidence indicating that food supply was not atypical during this time comes from egg volumes measured from this same random sample of Nazca boobies. Egg volumes either did not differ between years, or were larger in 1997. Therefore, food supplements increased clutch size under normal food availability, and they increased clutch size above that from any of the seven years for which comparable clutch size data exist (Fig. 1). This contrasts with other supplemental feeding experiments which have only increased clutch sizes when conditions were poor, and only to levels observed in good years or on good territories (Boutin 1990; Nager, Ruegger & van Noordwijk 1997). The Nazca booby data indicate that food limitation influences clutch size of some individuals even in an average or good food year.

In addition to receiving supplemental food, Nazca boobies in this study also spent less time, and presumably expended less energy, foraging. The observed increase in clutch size could therefore result from increased energy availability through decreased foraging effort and increased food supply, or alternatively, from the increase of a particular nutrient in the diet. Several studies suggest that clutch size is not limited by energy, but by protein or some other nutrient (Bolton, Houston & Monaghan 1992; Ramsay & Houston 1997; Meijer & Drent 1999). In either case, provision of extra fish released most females from the limitation.

In addition to increasing their clutch size, supplemented females also laid larger B-eggs than did control females. Most supplemental feeding experiments have not demonstrated an increase in egg size (Meijer & Drent 1999), with some exceptions (magpie *Pica pica*, Högstedt 1981; American kestrel *Falco sparverius*, Wiebe & Bortolotti 1995; American coot *Fulica americana*, Hill 1988; lesser black-backed gull *Larus fuscus*, Hiom *et al.* 1991; Bolton *et al.* 1992; glaucous-winged gull *Larus glaucescens*, Reid 1987). In this study, B-egg volume was not related to hatching success, and therefore increases in B-egg size did not affect hatching success. Instead, increased egg volume increased the hatchling mass of the B-chick. Several studies have demonstrated a positive effect of egg-size on offspring fitness mediated through hatchling size (Nisbet 1978; Bolton 1991; Magrath 1992). Therefore, supplemented females allocated nutrients from supplemental food to

increasing the quality of the B-chick, and not to the A-chick nor to adjusting hatching interval.

B-egg size in supplemented Nazca booby females was increased above that observed in 7 years of a long-term study at this same site (Fig. 2). Considering that egg volumes of unsupplemented females were relatively large in the year of the experiment, it appears that the supplemental food increased B-egg volume above that found in an average, or even good, food year, providing further evidence of proximate food limitation on egg production.

Pre-hatching influences on clutch size have frequently been ignored because the demands of brood-rearing have been thought to be much greater than those of the laying and incubation periods. However, increasing evidence indicates that both incubation and egg-production are demanding in terms of energy and nutrients (review in Monaghan & Nager 1997). Female lesser black-backed gulls (*L. fuscus*) forced to lay an additional egg produced a last-laid egg of lower quality than did control females (Monaghan, Bolton & Houston 1995), and experimental females finished the egg-laying period in poorer physiological condition than did control females (Monaghan *et al.* 1998). Larger clutches of supplementally fed female Nazca boobies and some other taxa further indicate that egg-laying is costly, and should be considered carefully in studies of clutch size evolution.

This experiment indicated that Nazca boobies do not always take advantage of an insurance egg because they are nutritionally limited. Selection appears to favour one-egg clutches for females below a threshold level of food limitation. Clearly, most females with single-egg clutches were not constrained to lay one egg, since 30% of control females laid one egg and only 8% of supplemented females did. Completing the picture of selection on clutch size, three-egg clutches are apparently not produced because the cost of the third egg would outweigh the additional benefit of another insurance egg (Anderson 1990). Together, nutritional limitation and the insurance value of second-laid eggs explain nearly all of the observed clutch size variation in Nazca boobies. Other factors must play a minor role in this system; however, as 8% of supplemented females did not produce a second egg. A slight effect of age on Nazca booby clutch size has been observed, with young and old parents producing smaller clutches (Clifford and Anderson, unpublished data). Therefore, correlates of age unrelated to short-term food intake may account for the remaining unexplained variation in clutch size.

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