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### What is the Function of First Eggs in Crested Penguins?

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Crested penguins (genus *Eudyptes*) have attracted considerable attention for the small size of their first-laid eggs. Depending on the species, the first egg is 15 to 45% smaller than the second (Warham 1975), the largest dimorphism known in birds (Slagsvold et al. 1984). Disadvantages accrued by smaller size are accentuated by reversed hatching asynchrony (first eggs hatch after second eggs), thereby defining an atypical system of brood reduction in which first eggs seldom survive to produce a fledgling. In other brood-reducing nonpasserines, egg size decreases with laying order, and first-laid eggs are more likely to survive (see Slagsvold et al. 1984, Williams 1994). These differences have prompted two unanswered questions concerning crested penguins (Johnson et al. 1987, Lamey 1990): why are first eggs smaller, and why are two eggs produced?

Questions about the function of first eggs are encouraged by the exceptional patterns of egg loss in three of the six species of *Eudyptes*. In Macaroni Penguins (*E. chrysolophus*; Gwynn 1953, Williams 1980, Williams 1989), Royal Penguins (*E. schlegeli*; Carrick 1972, St. Clair et al. 1995), and Erect-crested Penguins (*E. sclateri*; Richdale 1941, Miskelly and Carey pers. comm.), first eggs typically disappear from nests soon after laying. Most of these losses occur immediately before second eggs are laid (Williams 1989, St. Clair et al. 1995), and deliberate ejection by

female parents is the overwhelming cause of this mortality in Royal Penguins (St. Clair et al. 1995). Such early losses preclude most of the insurance or replacement function of first-laid eggs (sensu Mock and Parker 1986, Forbes 1991, Mock and Forbes 1995), and the timing of losses suggests that whatever function first eggs have is limited to the four-day laying interval between first and second eggs. Functions during this time may include limited insurance against occasional failure to lay a second egg (Williams 1989, St. Clair and St. Clair 1996), or secondarily derived functions that do not require the continued survival of first eggs. Because crested penguin eggs likely are inexpensive to produce (Williams 1990), and much selective inertia would attend the evolution of a single-egg clutch (St. Clair et al. 1995), even weak secondary functions during the laying interval may confer measurable benefits.

Several secondary functions have been suggested, although none has yet been tested. For example, first eggs may: (1) provide a signal to conspecifics that the nest site is occupied (Johnson et al. 1987), thus reducing contests over nesting space prior to the laying of the second egg; (2) enhance laying synchrony (Johnson et al. 1987) by providing a visual stimulus that quickens laying by surrounding pairs; (3) enhance mate attraction for young or first-time breeders by providing a visual indication of a female's preparedness to reproduce; and (4) provide an important tactile stimulation for formation of the brood patch (i.e. incubation patch), thereby enhancing the thermal environment of second eggs (St. Clair 1992). This secondary function could operate in both sexes but might be particularly important in males be-

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cause they share the early incubation in all crested penguin species (Warham 1975) and presumably have few other cues about the reproductive stage of their mates. It is this last hypothesis that I test here.

Anecdotal evidence that first eggs might provide an important stimulus for brood-patch formation was suggested during a cross-fostering event in 1989, when I provided a nonbreeding pair of Fiordland Crested Penguins (*E. pachyrhynchus*) with the abandoned first egg of a nearby nest (St. Clair 1990). The nonbreeding pair had been banded and had bred successfully in the previous year, but natural destruction of their nest site during the preceding winter likely inhibited their subsequent breeding. Following provisioning of the abandoned egg, the female developed a full brood patch and incubated the egg continuously for 25 days. During this period, I twice recorded incubation temperatures for a 24-h period with a thermocouple inserted into a preserved penguin egg (see St. Clair 1992). The nonbreeding bird produced a full brood patch and provided mean incubation temperatures that were within 3°C of those recorded for breeding birds (St. Clair 1990). Because this nest site had been checked daily, and I was confident that the nonbreeding bird had laid no egg of her own, I concluded that it was the stimulus of the egg that had initiated brood-patch formation and effective incubation behavior. Tactile stimulation from the nest cup or eggs is assumed to enhance patch formation in other bird species through mediating the release of prolactin (see Jones 1971, Goldsmith 1983, Williams et al. 1996). Thus, I predicted that crested penguins that were denied contact with their first eggs would exhibit retarded incubation capacity at the time their second eggs were laid and possibly later. Such an enhancement of brood-patch formation potentially would explain the retention of first eggs in species for which they are immediately ejected and have no other apparent function.

**Methods.**—The study was conducted with Rockhopper Penguins (*E. chrysocome*) on New Island, Falkland Islands, during November 1993. This species is intermediate within the genus *Eudyptes*, exhibiting egg dimorphism of about 25% and rates of first-egg mortality from 15 to 90% (77% in the year of this study; St. Clair and St. Clair 1996). Because I had previously found that it was more accurate and less disruptive to measure brood-patch formation indirectly by monitoring incubation temperatures (vs. directly by patch measurement; St. Clair 1992), I assessed incubation capacity through the temperatures of artificial eggs substituted in penguin nests. Artificial eggs consisted of a plastic two-piece hobby egg, approximately the same size as first eggs of Rockhopper Penguins, containing a Hobo<sup>®</sup> temperature data logger surrounded by a plaster casing. Plastic eggs were attached to a 5-cm lead of fishing line and anchored to the nest with a metal spike to deter care-

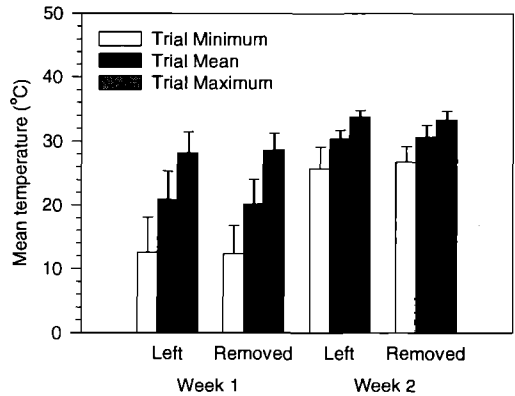


FIG. 1. Minimum, mean and maximum temperatures ( $\pm 1$  SE) recorded from nests where first eggs had been removed as they were laid or left in their nests during the four-day laying interval. Temperatures were recorded on the days second eggs were laid (week 1) or one week (1 day) later (week 2).

less parents and egg-robbing Great Skuas (*Catharacta skua*).

To measure the temperature effects of the presence of first eggs, I divided 26 nests into two treatment groups; on the day each first egg was laid, I either: (1) removed it, or (2) left it in place. I alternated assignments to match treatments by laying date. Some removed eggs were used in egg-content analysis (St. Clair 1996), but most were later returned to the colony. Temperature trials were conducted twice at each nest, once on the day the second egg was laid and once more a week later. During trials of approximately 12 or 24 h, I temporarily removed the natural egg(s) and replaced it with a temperature-logging egg. Egg temperatures were recorded each 4.8 min with the first hour after placement eliminated from the record to allow for equilibration of egg temperature. From each trial, I calculated the minimum, mean, and maximum temperatures and compared these between treatments to assess the importance of the first egg. Minimum and maximum ambient temperatures were recorded from a mercury thermometer during week 1 as part of another study.

**Results.**—There were no detectable differences in mean incubation temperatures at nests where first eggs were left compared with those where first eggs were removed (independent *t*-tests with *df* = 23 throughout; week 1,  $t = 0.41$ ,  $P = 0.68$ ; week 2,  $t = 0.30$ ,  $P = 0.77$ ; Fig. 1). Similarly, there were no differences in minimum temperatures (week 1,  $t = 0.10$ ,  $P = 0.92$ ; week 2,  $t = -0.96$ ,  $P = 0.92$ ; week 2,  $t = 0.96$ ,  $P = 0.35$ ), maximum temperatures (week 1,  $t = -0.34$ ,  $P = 0.74$ ; week 2,  $t = 0.81$ ,  $P = 0.42$ ), or within-trial temperature variance (week 1,  $t = 0.06$ ,  $P = 0.96$ ; week 2,  $t = 0.76$ ,  $P = 0.45$ ) for the two treatments.

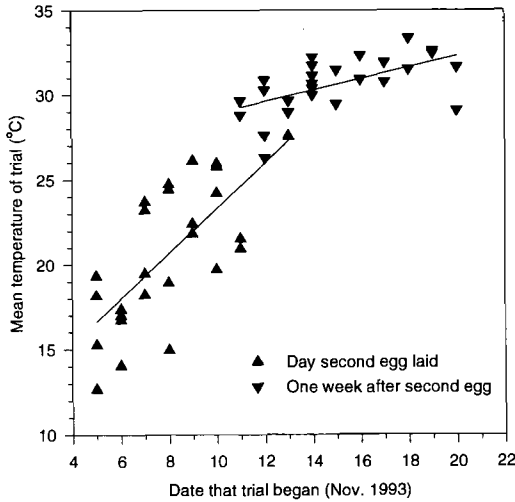


FIG. 2. Mean egg temperatures on the days second eggs were laid and one week later relative to the calendar date on which the temperature trial began. Regression statistics separated by weeks are given in the text.

In contrast, mean incubation temperatures increased steadily with advancing laying date during both week 1 (adjusted  $r^2 = 0.47$ ,  $n = 26$ ,  $P < 0.001$ ; Fig. 2) and, to a lesser extent, during week 2 (adjusted  $r^2 = 0.30$ ,  $n = 26$ ,  $P = 0.002$ ; Fig. 2). This relationship was not caused by seasonal increases in ambient temperatures, which did not contribute significantly in a stepwise multiple linear regression model ( $t = 0.62$ ,  $P = 0.54$ ). In an ANCOVA with laying date as the covariate, treatment (left vs. removed) still had no effect on mean incubation temperatures during week 1 ( $F = 0.16$ ,  $n = 26$ ,  $P = 0.69$ ) or week 2 ( $F = 0.30$ ,  $n = 26$ ,  $P = 0.58$ ), although laying date remained highly significant in these analyses (week 1,  $F = 22.34$ ,  $P < 0.001$ ; week 2,  $F = 11.65$ ,  $P = 0.002$ ). Finally, failure to detect a biologically meaningful effect of egg treatment was unlikely to have been caused by low statistical power; the sample size and variance of week 1 yielded a 90% chance of detecting an effect size  $\geq 20\%$  between treatment means.

**Discussion.**—I found no evidence that the first egg functioned to stimulate brood-patch formation or otherwise affected the incubation capacity of nesting Rockhopper Penguins. I suggest two interpretations of these negative results. First, incubation temperatures may not have responded to egg treatment because other stimuli were responsible for eliciting brood-patch development. Although it is generally accepted that incubation capacity is effected through increases in circulating levels of prolactin (Jones 1971, Goldsmith et al. 1984, March et al. 1994), the role of the nest and eggs in stimulating this change (*sensu* Jones 1969) is less certain. Anaesthetizing the brood

patch in domestic ducks (*Anas platyrhynchos*) caused significant drops in plasma prolactin (Hall and Goldsmith 1983), indicating that tactile stimulation of the brood patch was important in maintaining prolactin levels. However, such stimulation may be provided by the nest itself because several species exhibit drops in prolactin when they are deprived of their nests, whether or not the nests contain eggs (El Halawani et al. 1980, Goldsmith 1991, LeBoucher et al. 1993). In albatrosses (*Diomedea* spp.), neither the nest nor the egg seems to provide a necessary stimulus to maintain prolactin levels (Hector and Goldsmith 1985).

Thus, a second explanation for my negative results is that brood-patch formation and incubation capacity are mediated through alternative pathways in penguins: tactile stimulation may not play a role in brood-patch development and/or prolactin may not be responsible for initiating incubation behavior. In Macaroni Penguins and Gentoo Penguins (*Pygoscelis papua*), circulating level of prolactin peak much later in the incubation period than is typical of other birds, and surges of the gonadal steroids estradiol and progesterone actually may be more important in prompting the onset of incubation behavior (Williams 1992, Williams and Sharp 1993). Similar peaks in these hormones have been found in Ringed Turtle-Doves (*Streptopelia risoria*; Lea 1987) and King Penguins (*Aptenodytes patagonicus*; Cherel et al. 1994), the only other species known to exhibit retarded increases in prolactin levels (Goldsmith 1991). Clearly, more work is needed to determine which factors are responsible for the initiation and maintenance of both brood-patch development and incubation behavior in penguins and the potential differences in these mechanisms among species.

If a different mechanism of incubation initiation exists in penguins, it also may be responsible for the strong relationship I found between incubation temperatures and laying date. Similar increases in early incubation temperatures have been recorded in other crested penguins (Burger and Williams 1979, Brown 1988, St. Clair 1992) and Yellow-eyed Penguins (*Megadyptes antipodes*; Farner 1958). In these studies, it is difficult to separate the effects of embryo age and calendar date, but a reanalysis of data from Fiordland Crested Penguins (St. Clair 1992) revealed that temperature increases during the first week of incubation were due partly to laying date (multiple linear regression, adjusted  $r^2 = 0.87$ ,  $df = 2$  and  $7$ ,  $t = 3.06$ ,  $P = 0.018$ ; embryo age,  $t = 4.41$ ,  $P = 0.003$ ). This correlation occurs over a remarkably short period of time (eight days in this study), suggesting that a strong exogenous signal is involved. The most obvious of these, a corresponding increase in ambient temperature, was not responsible for the increases in incubation temperature, but two other factors potentially are involved.

First, incubation temperatures may increase with laying date in response to photoperiod (Haywood

1993). Prolactin secretion is directly affected by photoperiod in nestling and juvenile starlings (Williams et al. 1987), and this relationship may be fairly universal in birds (Meijer et al. 1990). However, photoperiod effects usually are measured over weeks or even months. In colonial, synchronous species like penguins, the role of photoperiod may be superseded by a second factor, the social stimuli from conspecifics. Waas (1995) used playbacks of courtship calls and other colony sounds to decrease the amount of time required for egg formation and increase the laying synchrony of Little Blue Penguins (*Eudyptula minor*) and Royal Penguins, indicating that these birds are highly responsive to social stimuli. I propose that a similar mechanism is responsible for the higher incubation temperatures of later nesters in this study: Later-nesting birds benefit from the cumulative stimuli provided by conspecifics, and they begin incubation at a relatively more developed stage.

A causal link between social stimuli and incubation capacity has important evolutionary implications for crested penguins. If earlier-laid eggs experience lower incubation temperatures, then an individual penguin necessarily discriminates against its own first-laid egg because incubation effectiveness always will be greater when its second egg is laid. The temperature advantage accrued in a few days appears to be substantial, because the higher incubation temperatures exhibited by later-nesting birds in this study presumably also account for the shorter incubation period of later-laid eggs in Rockhopper Penguins (St. Clair 1996). Thus, socially facilitated increases in incubation temperature may contribute to the reversal in both hatching asynchrony and, secondarily, egg dimorphism that are unique to crested penguins. More work will be needed to determine what function, if any, first eggs serve during the brief interval for which they typically are retained in all species of crested penguins.

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