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Received 16 August 1999, accepted 10 February 2000.
Associate Editor: T. W. Arnold

The Auk 117(3):817–820, 2000

Insurance Eggs versus Additional Eggs: Do Brown Boobies Practice Obligate Siblicide?

BERNIE R TERSHY,^{1,2,3} DAWN BREESE,² AND DONALD A. CROLL²

¹Section of Neurobiology and Behavior, Cornell University, Ithaca, New York 14853, USA; and

²Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA

At least 22 species of birds in 8 families frequently lay two or more eggs but typically fledge only one chick (Anderson 1990a). Brood reduction is caused by the senior chick attacking the junior chick and killing it directly, or killing it indirectly by keeping it from feeding or by forcing it from the nest (Mock et al. 1990). Although brood reduction should provide a fertile arena for observing parent-offspring conflict (*sensu* Trivers 1974), no evidence exists that parents attempt to stop siblicide, suggesting that parents have conceded the conflict to senior chicks (Drummond 1987, Anderson 1990b, Forbes 1991, Mock and Forbes 1992).

If senior chicks invariably kill junior chicks with no interference from parents (i.e. obligate siblicide), why do females frequently invest in second eggs?

Dorward (1962) developed the insurance-egg hypothesis to explain this apparent paradox in the Brown Booby (*Sula leucogaster*) and Masked Booby (*S. dactylatra*). As reformulated by Anderson (1990a), the insurance-egg hypothesis states that females can be selected to lay more than one egg when junior chicks sometimes fledge after embryos or hatchlings from first-laid eggs die. Consistent with the insurance-egg hypothesis are studies in eight species where 2 to 22.0% of fledglings are produced by second eggs when the first eggs fail to hatch or the first chicks die (Anderson 1990a).

An alternative (but not mutually exclusive) is the additional-egg hypothesis, which states that females can be selected to lay a second egg when offspring from both eggs sometimes fledge. The additional benefit of second eggs is most likely to occur in years of exceptionally high food availability and to be enjoyed by high-quality parents. The insurance-egg hypothesis should apply to all years and all parents with two-egg clutches (Simmons 1988).

³ Present address: Institute of Marine Sciences, University of California, Santa Cruz, California 95064, USA. E-mail: tershy@cats.ucsc.edu

Several studies of Masked Boobies have provided data that support the insurance-egg hypothesis (Kepler 1969, Nelson 1978, Woodward 1972, Anderson 1990a). Two studies of Brown Boobies breeding in the central Pacific (Woodward 1972, Amerson and Shelton 1976) have determined that second-laid eggs have substantial insurance value, with 12 to 16% of second-hatched chicks fledging from two-egg clutches when the first chick died. These studies also showed that 1 to 3% of second-hatched chicks in two-egg clutches fledged in addition to the senior chick.

We measured and compared the value of insurance eggs and additional eggs in a study of Brown Boobies nesting on San Pedro Mártir Island, Mexico. First, we calculated hatching success to determine the potential value of an insurance egg in response to egg failure. Second, we determined the longevity of junior chicks to determine how long the second chick provides insurance against death of the first chick. Third, we tested whether longevity of junior chicks affects fledging success of senior chicks to measure one potential cost of this insurance. Finally, we calculated the insurance value of second eggs in 1991 and the overall additional value of second eggs in 1990, 1991, and 1993.

Study area and methods.—Research was conducted for a total of nine months on San Pedro Mártir Island, Gulf of California, Mexico (28°23'N, 112°20'W) in 1990, 1991, and 1993. San Pedro Mártir is a steep, 1.9-km² desert island with a maximum elevation of 305 m. It supports the largest known colony of Brown Boobies, with 30,000 to 50,000 nesting pairs (B. Tershy et al. unpubl. data). We had four adjoining study plots that contained 110 to 204 nests (plots ranged from 1,000 to 4,225 m²). We mapped each plot, marked the location of all nests, and visited each nest at least once a week during the roughly 42-day incubation period and the 90-day nestling period. We considered a chick to be fledged when it weighed at least 1 kg, and the only down not replaced by contour feathers was on the head and flanks.

In 1991, we visited nests more frequently near the end of incubation and during the first few weeks of chick growth to record the fate of individual eggs and chicks. We recorded the order in which eggs were laid and marked them with a permanent marking pen. To keep track of first and second chicks at each nest, we banded chicks with progressively larger temporary plastic color bands until chicks were close to fledging and could be banded with a numbered metal band.

We did not systematically observe and record siblicidal behavior, but on occasion we saw senior chicks pecking at junior chicks, found dead junior chicks in the nest, and found live junior chicks outside the nest. Most deaths or disappearances of junior chicks resulted from injury caused by senior chicks, starvation from competition with senior chicks, or predation and exposure after being forced

from the nest by senior chicks (see Dorward 1962, Woodward 1972, Amerson and Shelton 1976, Nelson 1978, Drummond 1987).

Results.—In 1991, hatching success of eggs from one-egg and two-egg clutches was 63.6% (178 of 280 eggs). Of the 102 eggs that did not hatch, 73 (71.6%) disappeared (primarily from predation by Yellow-footed Gulls [*Larus livens*] and Common Ravens [*Corvus corax*]), and 29 (28.4%) failed to hatch for unknown reasons. We opened six of the latter eggs when they were at least 50 days old, and none had visible developing embryos.

Of the 127 nests with two-egg clutches in 1991, both eggs hatched in 63 nests (49.6%), one egg hatched in 34 nests (26.8%), and no eggs hatched in 30 nests (23.6%; most egg losses were from predation). When only one egg hatched in two-egg clutches, it was just as likely to be the first-laid egg ($n = 17$) as the last-laid egg ($n = 17$). When both eggs hatched, the junior chick disappeared or was found dead within one week in 41 of 63 nests (65.1%). In these 41 nests, 22 (53.7%) senior chicks fledged. In the 22 nests where both chicks survived past one week, 14 (63.6%) senior chicks fledged. The fledging rate for senior chicks in these two groups was not significantly different ($\chi^2_c = 0.246$, $df = 1$, $P = 0.62$). Of the 41 nests with two-egg clutches in 1991 where we knew which egg fledglings came from, 33 (84.6%) produced a fledgling from the first egg, 6 (14.6%) produced a fledgling from the second egg, and 2 (4.9%) produced fledglings from both eggs.

For all three years combined, 100 nests with two-egg clutches fledged young. Of these, seven (7.0%) fledged two young. Fledging success of the second chick in two-egg clutches differed by year: 0 of 24 successful nests fledged two chicks in 1990, 2 of 44 fledged two chicks in 1991, and 5 of 24 did so in 1993. Ranking years according to the proportion of two-egg nests that fledged at least one chick, the best year, 1993 (37% of nests fledged at least one chick), also was the year in which the highest proportion of two-egg clutches fledged both young (21%). Moreover, the worst year, 1990 (19% of nests fledged at least one chick), was the year in which the lowest proportion of two-egg clutches fledged two young (0%). Results in 1991 were intermediate: 35% of nests fledged at least one chick, and 5% of two-egg clutches fledged both chicks.

Discussion.—Hatching success of Brown Boobies on San Pedro Mártir was low and comparable to values elsewhere: 61.2% on Kure Atoll (Woodward 1972), 63% on Johnston Atoll (Amerson and Shelton 1976), and 51% on Christmas Island in the Indian Ocean (Nelson 1978). Possible proximate causes of low hatching success are discussed by Anderson (1990a). Low hatching success is consistent with the insurance-egg hypothesis because it indicates the potential need for an insurance egg. In nests with two-egg clutches, hatching failure or egg loss affect-

ed both eggs in 23.6% of the nests and one egg in 26.8%. Thus, roughly one clutch in four had the potential to receive an insurance benefit from the second egg prior to hatching.

When both eggs hatched, the second chick provided insurance against the death of the first chick for less than one week in 65% of the nests and for more than one week in the remaining 35% of nests. For senior chicks, theory predicts a tradeoff between benefits from kin selection of junior chicks providing insurance, and direct fitness costs of competition with junior chicks (Mock et al. 1990). During chick development, benefits from kin selection should remain constant, or even decrease depending on the probability that the senior chick survives. In contrast, direct fitness costs may increase because larger chicks require more food to meet their metabolic demands. This cost is heightened if the probability of dominance reversals between senior and junior chicks, or the cost of dominance per se, increases with chick age. Siblicide is expected to occur when direct fitness costs surpass benefits from kin selection. As an initial exploration of this hypothesis, we examined, but found no evidence for, a survival cost to the senior chick for extending the duration of survival of the junior chick past the period when most siblicide occurred (i.e. one week). This was not a critical test, however, because decreased fledging success is not the only potential direct fitness cost of extending the survival of junior chicks. Postfledging survival and reproductive success of senior chicks also may be affected.

In 1991 on San Pedro Mártir, the insurance value of second eggs (i.e. proportion of two-egg clutches in which only the chick from the second egg fledges) was 14.6%, and the additional value of second eggs (i.e. proportion of two-egg clutches in which both chicks fledge) was 4.9%. The additional value of second eggs during the entire study was 7%. We do not have a comparable overall value for insurance eggs because we followed the fate of individual eggs only in 1991. The insurance and additional values of second eggs for Brown Boobies were 16.3% and about 1.3%, respectively, on Kure Atoll (Woodward 1972) and 12% and about 2.8%, respectively, on Johnston Atoll (Amerson and Shelton 1976). The slightly higher additional value of second eggs on San Pedro Mártir compared with Kure and Johnston atolls may be due to high primary productivity and prey abundance in the Gulf of California compared with the central Pacific (Alvarez-Borrego 1983). All things being equal, this should allow Brown Boobies to provision two chicks more often on San Pedro Mártir than on Kure and Johnston atolls.

Ever since Dorward (1962), the Brown Booby has been considered to practice obligate siblicide (Drummond 1987, Anderson 1990a). However, in some years we found a considerable additional value of second eggs. If adults can fledge two chicks without

disproportionately decreasing their future reproductive success, then selection should result in relaxed siblicidal behavior in response to conditions that allow both chicks to fledge. Parental quality and prey availability could influence the ability of adults to fledge two offspring.

The additional-egg hypothesis predicts that higher-quality parents will fledge two offspring more often than lower-quality parents and that the proportion of successful nests that fledge two chicks will be higher in years of high food availability. Our limited data suggest that in years when a higher percentage of nests are successful, more successful nests fledge two chicks. Although not a direct measure of prey availability, fledging success probably is related to prey availability because most chick mortality results from starvation (B. Tershy unpubl. data). If a clear relationship between parental quality or food availability and the frequency of successful nests that fledge two chicks can be demonstrated, this would support the additional-egg hypothesis, and the Brown Booby would be classified as facultatively siblicidal, at least in some populations.

If Brown Boobies are facultatively siblicidal, mechanisms should exist that alter siblicidal behavior. Adults potentially could vary the competitive advantage of the senior chick, and therefore the probability of siblicide, by adjusting egg size, laying interval, or the start of incubation. On San Pedro Mártir, first eggs are larger than second eggs (Tershy 1998), as has been found in other populations of Brown Boobies, but we have no data on laying intervals or the timing of incubation. Alternatively, senior chicks could alter their siblicidal behavior in response to indicators of their parents' provisioning abilities. Drummond and Garcia Chavelas (1989) demonstrated that senior chicks of the facultatively siblicidal Blue-footed Booby (*S. nebouxii*) are siblicidal when their body mass decreases below a threshold level. Brown Booby chicks on San Pedro Mártir may have a similar response, but presumably at a higher threshold.

In conclusion, the insurance-egg and additional-egg hypotheses are not mutually exclusive in explaining the maintenance of two-egg clutches in siblicidal birds. Our data support both hypotheses in a population of Brown Boobies on San Pedro Mártir Island. Support for the additional-egg hypothesis raises the possibility that Brown Boobies have been inappropriately labeled as practicing obligate siblicide. Further studies should examine the possibility of facultative siblicide in this species.

Acknowledgments.—Field work was funded by Conservation International Mexico, American Ornithologists' Union, Los Angeles Audubon Society, Bird-Life International, Sigma-XI, Frank M. Chapman Fund, Explorers Club, Cornell Graduate School, and an NIMH Training grant to BRT. Research was conducted under Secretaría de Desarrollo Urbano y

Ecología permit numbers 0492, 00987, and 11782. We thank the Secretaría de la Marina, Sexta Zona Naval, Guaymas, for transportation and food deliveries. For logistic support, we are indebted to the Instituto Tecnológico y de Estudios Superiores de Monterrey-Campus Guaymas, Rescue One, A. Robles, E. Velarde, J. Guzman, L. Gonzales, Prescott College, Baja Expeditions, Special Expeditions, H. and V. Ballance, and T. Pfister. We are grateful to Eureka Tents, Ocean Kayaks, S. Emlen, J. Guzman, and E. Velarde, for use of research equipment. We especially thank D. Able, A. Angeles, S. Ashe, X. Basurto, G. Brabata, C. Carmona, M. Cervantes, D. Craig, G. Fernández, K. Mingo, C. Navaro, N. Nuñez, H. Pérez, and E. Tobón for excellent help and company in the field. We are grateful to D. Anderson, H. Drummond, and BRT's graduate committee members E. Adkins-Regan, S. Emlen, T. Gavin, P. Sherman, and D. Winkler for their excellent reviews of the manuscript.

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Received 23 March 1998, accepted 10 February 2000.
Associate Editor: T. W. Arnold

The Auk 117(3):820-825, 2000

The 20-cm Spiny Penis of the Argentine Lake Duck (*Oxyura vittata*)

KEVIN G. MCCracken¹

School of Forestry, Wildlife, and Fisheries, Louisiana State University, Baton Rouge, Louisiana 70803, USA

The genitals of male birds generally are not noted for their size or extravagant ornamentation. For most species of birds, well-developed penes or intromittent organs are absent (e.g. King 1981, Briskie and Montgomerie 1997). Sperm transfer occurs via the

mutual juxtaposition of the protruded cloacae, and there is relatively little contact between males and females compared with the process of coital penetration in mammals, reptiles, some species of fish, and most insects (Eckstein and Zuckerman 1956, Dowling and Savage 1960, Eberhard 1985). Several groups of birds, including ratites, screamers, waterfowl, and cracids, possess well-developed male copulatory organs (Forbes 1882, King 1981, Lake 1981). In these groups, the penis (or male intromittent organ) arises

¹ Present address: University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, USA. E-mail: fnkgm@uaf.edu