ARE DAILY MORTALITY RATES FOR REAL AND ARTIFICIAL CLUTCHES COMPARABLE?

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Resumen. – ¿Son comparables las tasas de mortalidad diaria de las nidadas naturales y las nidadas artificiales? – Determinamos si la tasa de mortalidad diaria (tmd) de las nidadas artificiales de huevos de pinzones (*Taeniopygia guttata*) y de codornices (*Coturnix japonica*) es similar a la tmd de las nidadas naturales del Yigüirro Collarejo (*Turdus assimilis*), en Costa Rica. En el año 2002, encontramos y monitoreamos nidos de yigüirros hasta que los pichones salieran del nido o hasta que la nidificación fracasara. Después de que cada intento de nidificar terminó, colocamos un huevo de pinzón y un huevo de codorniz en cada nido y monitoreamos los nidos durante 14 días. La tmd de las nidadas del yigüirro fue más baja que la de las nidadas artificiales. Los resultados (sobrevivió o no sobrevivió hasta la eclosión) de las nidadas naturales y las artificiales no presentaron ninguna correlación. Al considerarlos por separado, los huevos de pinzones tuvieron una tmd más alta que la de las nidadas naturales y de los huevos de codornices. Los resultados de los huevos de pinzones y de las nidadas naturales no presentaron ninguna correlación. La tmd de los huevos de codornices fue similar a la tmd de las nidadas naturales, aunque no se encontró ninguna correspondencia entre los resultados de las nidadas naturales y de los huevos de codornices. Los huevos de pinzones no son modelos buenos para esta especie debido a su alta susceptibilidad a la depredación. Los huevos de codornices pueden ser modelos razonables si la depredación en los nidos de los yigüirros es un proceso al azar.

Abstract. – We determined if the daily mortality rate (dmr) for artificial clutches of Zebra Finch (*Taeniopygia guttata*) and Japanese Quail (*Coturnix japonica*) eggs matched the dmr of real clutches of the White-throated Robin (*Turdus assimilis*), in Costa Rica. In 2002 we found and monitored robin nests until fledging or failure. After each nesting attempt ended, we placed one finch egg and one quail egg in the nest and monitored the nest for 14 days. The dmr for the robin clutches was lower than the dmr for the artificial clutches. The outcomes (survived or did not survive until hatching) for the real clutches and the artificial clutches did not correspond. When finch eggs and quail eggs were considered separately, finch eggs had a significantly higher dmr than both the real clutches and the quail eggs and there was no correspondence between the outcomes of the finch eggs and the real clutches for individual nests. The quail egg dmr was similar to the dmr of the real clutches, although there was no correspondence between the outcomes for the real clutches and the quail eggs for individual nests. Finch eggs are not a good model for this species because of their high susceptibility to predation. Quail eggs may be a reasonable model if predation on White-throated Robin nests is a largely random process. *Accepted 27 October 2003.*

Key words: Artificial clutches, Costa Rica, daily mortality rate, nest success, White-throated Robin, Japanese Quail eggs, *Turdus assimilis*, Zebra Finch eggs.

INTRODUCTION

Studies using artificial nests have been conducted to document spatial patterns of nest predation (Gibbs 1991, Söderström *et al.* 1998, Vander Haegen *et al.* 2002), to investigate interspecific differences in susceptibility to predation (Sieving 1992), and to investigate the influence of parental behavior on the likelihood of nest predation (Cresswell 1997, Martin *et al.* 2000). If results from artificial nests provided reasonably good information regarding mortality patterns on real nests, investigators would be able to augment their sample sizes and control for a number of variables that are difficult to control for when working with real nests. However, a number of issues have been raised regarding the application of artificial nests to investigations of nest mortality (Major & Kendal 1996, Wilson *et al.* 1998). Recent investigations indicate that predation patterns on artificial nests may not accurately reflect patterns on real nests, calling into question the usefulness of artificial nest studies (Weidinger 2001, Pärt & Wretenberg 2002, Zanette 2002, Roper 2003).

One reason that the fates of artificial nests may not accurately mimic the fates of real nests is differences between the experimental clutches and those of the species that actually inhabit an area. Artificial clutches often include eggs of Japanese Quail (*Coturnix japonica*) or Zebra Finches (*Taeniopygia guttata*). Quail eggs are larger than the eggs of many passerine species they are expected to mimic while Zebra Finch eggs are smaller. Hence, quail eggs may be too large for some of the typical nest predators to remove or break, resulting in underestimates of predation rates (Roper 1992, Haskell 1995, Marini & Melo 1998) while the small finch eggs may be more easily breached than those of the target species, resulting in overestimates of predation rates (Maier & DeGraaf 2001).

In most previous investigations of the concordance of results between real and artificial nests, the real nests have differed from the artificial nests in several ways: egg type (eggs of resident species vs. artificial or quail eggs), nest site characteristics (artificial nests were placed in different sites than real nests), and nest type (real vs. artificial, e.g., Storaas 1988, Pärt & Wretenberg 2002, Zanette 2002). With these types of experimental designs, if daily mortality rates (dmrs) and/or fates differ between real and artificial nests, it is difficult to pinpoint the reason or reasons for the differences. One way to control for the effects of nest site and nest type on dmrs and fates is to compare these variables for real clutches in real nests to those for artificial clutches in the same nests after the real nesting attempts have succeeded or failed (e.g., Roper 2003). We followed this technique although, unlike previous investigations, we used clutches composed of two egg types, Japanese Quail and Zebra Finch, that are commonly used in artificial nest experiments. Because each nest received one quail and one finch egg, we were able to compare the dmrs and outcomes (survived or did not survive until hatching) for these two egg types. Our objectives were 1) to determine whether the dmrs and outcomes for the quail egg/finch egg artificial clutches were similar to the dmrs and outcomes for the real clutches, and 2) to determine whether dmrs for finch eggs and quail eggs, calculated separately, differed. We also compared the dmrs and outcomes for the finch eggs and the quail eggs, considered separately, to the dmrs and outcomes for the real clutches.

METHODS

The study took place from March through June of 2002 on a 10,000 ha farm, Las Alturas, in the Talamanca mountains of southern Costa Rica (8°57'N, 82°50'W). The farm comprises cattle pastures, abandoned coffee

plantations, forest, and second-growth vegetation and is surrounded by seasonal montane wet forest (Holdridge *et al.* 1971). The elevation at the site ranges from approximately 1300 to 1500 m.

The White-throated Robin (*Turdus assimilis*) nests in both forested and agricultural habitats. Its nesting season at Las Alturas begins in mid-March and continues through August, with a peak in May (Lindell unpubl.). The cup nests of the robin are constructed of vegetation and mud. We conducted the study with nests of this species because we could find enough nests at accessible heights to insure adequate sample sizes for statistical analyses.

Nest searching took place in the agricultural habitats within the farm, primarily within two pasture areas of approximately 25 ha total and several coffee areas of approximately 25 ha total, although nests in other areas were located on an ad-hoc basis frequently. When we located an active nest, it was marked with flagging more than 5 m from the nest and it was checked every two to four days until the nesting attempt failed or fledglings left the nest.

Zebra Finch eggs were supplied by a laboratory at Michigan State University and transported to Costa Rica, and quail eggs were purchased in San José, Costa Rica. The Zebra Finch eggs were smaller than the quail eggs in both mean length [15.3 ± 1.1 mm vs. 31.5 ± 1.2 mm (SD), respectively, n = 20] and mean diameter at the widest point [11.4 ± 0.5 vs. 24.7 ± 1.2 (SD), respectively, n = 20]. White-throated Robin eggs were intermediate in size [mean length = 29.4 ± 0.7, mean diameter = 20.5 ± 0.7 (SD), n = 6]. All eggs were infertile and were handled with latex gloves after acquisition. We placed one finch and one quail egg in each nest six to eight days after a nesting attempt ended (White-throated Robins have a modal clutch size of two, Lindell unpubl.). In one case we reconstructed the robin nest prior to egg placement. We placed

eggs in nests between 05:30 and 08:30 CST (except in one case, when eggs were placed at 09:15) and we noted any scratches or markings on eggs before we placed the eggs in the nests.

The egg stage of most White-throated Robin nests lasts between 13 and 15 days (Lindell unpubl.). Hence, we checked nests with artificial clutches on days 4, 7, 10, and 14 or until both eggs were no longer present (but not beyond day 14) or were damaged with punctures or breakage that would have made hatching unlikely if they had been real eggs. We examined eggs at each check and noted any new markings. We placed 61 artificial clutches between 6 April and 13 June.

Statistical analyses. We used the Mayfield method (Mayfield 1975) to estimate dmrs for the real and artificial clutches, considering results from the finch and quail eggs together. In other words, if the finch egg was gone by day 4, the clutch was considered to have failed by that point, regardless of whether the quail egg remained intact in the nest beyond day four. For the real clutches, we estimated the dmr for only the egg period. We also estimated dmrs for the finch eggs and the quail eggs separately. Because three quail eggs acquired superficial scratches after placement in nests, likely because a small rodent or marsupial tried but was unable to break the eggs, we calculated another dmr for the quail eggs considering these eggs preyed upon when the scratches were first noted (Marini & Melo 1998). We refer to this value as the conservative quail dmr.

We estimated variances and standard errors for the mortality rates following Johnson (1979). We determined whether dmrs were significantly different for the real and artificial clutches, and for the finch eggs versus the quail eggs, using the software program CONTRAST (Hines & Sauer 1989a, 1989b). The program compares rates using variance-

TABLE 1. Fates of finch and quail eggs in artificial clutches (N = 59).

Fate of egg by day fourteen	Finch eggs	Quail eggs
Present and intact	5	24
Missing	32	27
Missing, fragments found outside nest	2	0
Present, with crack or hole	5	1
Present, with crack or hole and insects present	5	0
Shell fragments found in nest	6	4
On ground outside nest (intact, or with crack or hole)	4	3

covariance matrices and tests for significant differences using the chi-square distribution. To calculate the number of exposure days for use in the Mayfield equations we assumed that nests that failed had failed midway between the last check and the next to the last check. We excluded from analyses results from two real/artificial pairs of clutches because observations strongly suggested that White-throated Robins trying to renest damaged the artificial clutches.

We considered a real clutch successful if it survived until hatching and an artificial clutch successful if it survived until day 14. To determine whether quail and finch eggs had outcomes that were associated with the outcomes of the real clutches in the same nests, we used contingency table *G*-tests of independence with Williams's correction (Sokal & Rohlf 1995). We also used this test to determine if the outcomes of the finch and quail eggs within nests were independent.

Values are given as means ± SE, unless noted otherwise. We considered a *P*-value of less than 0.05 as significant.

RESULTS

The majority (79.7%) of the real clutches were located in the primary nest searching areas of pasture and abandoned coffee with the remaining 20.3% located away from these areas, often in road banks.

All of the real clutches that failed showed evidence that predation was the cause of the failure, i.e., eggs were missing or damaged. The dmr for the 59 real clutches (8.0 ± 1.3%) was significantly lower than the dmr for the 59 artificial clutches (21.0 ± 2.5%; $\chi^2 = 20.4$, $P < 0.001$). The high dmr for the artificial clutches was primarily due to numerous losses of finch eggs. In 18 of the artificial clutches the Zebra Finch egg did not last until day 14 while the quail egg did (Table 1). In contrast, no cases existed of the quail egg being preyed upon and the Zebra Finch egg in the same nest subsequently lasting until day 14.

The dmr for the finch eggs alone (19.4 ± 2.4%) was significantly higher than the dmr for the quail eggs alone (7.6 ± 1.2%; n = 59, $\chi^2 = 19.4$, $P < 0.001$). The conservative quail dmr (7.9 ± 1.3%) was also significantly lower than the finch egg dmr (n = 59, $\chi^2 = 18.2$, $P < 0.001$).

The outcomes for the artificial clutches (Zebra Finch and quail eggs combined) were independent of the outcomes for the real clutches (n = 59, $G = 0.5$, df = 1, $P > 0.10$). Despite the fact that the quail egg dmr was very similar to the dmr for the real clutches, the actual outcomes for real clutches and the quail eggs were not more concordant than the outcomes for the real clutches and the finch eggs. In 54% of the cases, the quail eggs and the real clutch had the same outcome while, in 58% of the cases, Zebra Finch eggs had the same outcome as the real clutches. In both comparisons the outcomes were independent (quail eggs vs real clutches: n = 59, $G = 0.04$, df = 1, $P > 0.5$; finch eggs vs real clutches: n = 59, $G = 0.5$, df = 1, $P > 0.10$). The outcomes of finch and quail eggs within nests were not independent, with similar outcomes

in 68% of the cases (n = 59, G = 8.7, df = 1, P < 0.005). None of the results described in this paragraph change as a result of considering the three quail eggs with scratches as depredated when the scratches first appeared because all three of these eggs were eventually lost to predators.

We saw the following potential egg predators near nests: several lizard and snake species, red-tailed squirrels (*Sciurus granatensis*), and several bird species: Chestnut-mandibled Toucans (*Ramphastos swainsonii*), Fiery-billed Aracaris (*Pteroglossus frantzii*), and Emerald Toucanets (*Aulacorhynchus prasinus*). Other potential predators in the area include a variety of rodent species, several marsupial species, coatis (*Nasua narica*) collared peccaries (*Tayasu tajacu*), and white-faced capuchin monkeys (*Cebus capucinus*).

DISCUSSION

Nesting success is often associated with particular characteristics of nest sites (e.g., Dion *et al.* 2000, Kershner *et al.* 2001, Chase 2002, Roper 2003). In addition, nest type, i.e., real or artificial, has been shown to influence predation rates when egg type is held constant (Martin 1987, Weidinger 2001), as has egg type when nest type is held constant (Yahner & Mahan 1996, Bayne & Hobson 1999). Hence, differences in dmrs between real and artificial nests placed in different locations could be due to differences in any one of these variables. By comparing the dmrs and outcomes of real and artificial clutches in the same nests, we were able to control for potential differences in nest types and nest-site characteristics that might be confounded with egg-type effects on dmrs and outcomes.

Our finding that the dmr for the artificial clutches was higher than the dmr for the real clutches, primarily because of the high rates of loss and damage to the Zebra Finch eggs, is consistent with expectations that the finch eggs are more likely to be depredated by small predators that may be unable to breach the larger eggs of many passerine species (Roper 1992, Maier & DeGraaf 2001). This expectation is further supported by the high dmr of the finch eggs compared to the quail eggs. A larger range of nest predator species was apparently able to access the Zebra Finch eggs than the robin or quail eggs. For example, five finch eggs were found seriously damaged with small insects on and/or in them (four with ants, and one other with unidentified insects), but none of the quail eggs in the artificial clutches or robin eggs in the real clutches were damaged in this way. In two of these cases, initial damage may have been caused by some other factor and then the insects moved in, but in at least three we suspect the ants were the cause of small holes in the eggs. Also, in three cases quail eggs showed superficial scratches on the shell on the same day that the finch egg in the nest was missing or destroyed, suggesting that the animals that preyed on the finch eggs tried, but failed, to prey on the quail eggs.

A number of the potential egg predators at our site, including the large birds, snakes, and coatis, would likely have had no trouble preying on quail, finch, or robin eggs. A number of nesting failures over the years of our work at Las Alturas have shown evidence of predation by relatively large predators, e.g., nests being extensively damaged. However, the Robinson's mouse opossum (*Marmosa robinsoni*) was considered as an important predator on eggs of understory passerines in Panama (Roper & Goldstein 1997). The range of Robinson's mouse opossums does not extend into Costa Rica, but it is likely that the Mexican mouse opossum (*Marmosa mexicana*), which is similar in size to Robinson's and has been reported to prey on bird eggs, lives at our site (Alonso-Mejía & Medellín 1992). A Robinson's mouse opossum did not eat quail eggs in captivity although it had eaten smaller

eggs in the wild (Roper 1992). Hence, if the Mexican mouse opossum and/or small rodents are important nest predators on the eggs of small species at our site, and are unable to prey on robin or quail eggs because of their larger size, this may partially explain the difference in mortality rates between the finch eggs and those of the robin and quail eggs.

An alternative explanation for a higher dmr on the artificial clutches compared to the real clutches is that the eggs and/or nestlings from the real clutches left odors on the nests that made them easier for predators to find when they contained the artificial clutches. However, quail eggs considered separately did not show a higher dmr than the real clutches, indicating that egg characteristics (i.e., the small size and perhaps relatively greater fragility of the finch eggs compared to the robin eggs) are responsible for the difference in dmrs. This supposition also has support from the results of Roper (2003), in which Western Slaty Antshrike (*Thamnophilus atrinucha*) clutches in Panama had a higher dmr than artificial clutches composed of quail eggs. Antshrike eggs are smaller than quail eggs and it is likely that some of the typical predators on antshrike nests would not be able to eat quail eggs because of their size (Roper 1992).

Other studies have documented that dmrs for artificial nests do not consistently correspond with dmrs for real nests (e.g., Weidinger 2001, Zanette 2002, Pärt & Wretenberg 2002). In all cases, the authors suggested that the artificial eggs of plastic or plasticine used in the artificial nests were more prone to predation by particular subsets of predators compared to the real eggs. In the study by Pärt & Wretenberg (2002), predation risk on quail eggs, as opposed to plasticine plus quail eggs, did correspond with risk to real nests, likely because the quail eggs, and the real eggs that the quail eggs were supposed to mimic, were accessible to the same

predators.

Although we showed similar dmrs for robin clutches and quail eggs, the outcomes for the robin clutches and quail eggs were not correlated, although they were in the same nests. The concordance of the results between the robin clutches and quail eggs was not improved even when we considered the quail eggs with scratches depredated, as suggested to reduce the bias in information from artificial nests (Marini & Melo 1998). These results are similar to those of Roper (2003) where the fates of real clutches of the Western Slaty Antshrike were not related to those of quail eggs placed in antshrike nests after the real nesting attempts failed or succeeded. If nest predation is a random process, the pattern of predation on quail eggs in both our study and Roper's could be representative of the pattern on real clutches. Random nest predation may be particularly likely in areas with a species-rich nest predator guild, as is expected in tropical areas (Filliater *et al.* 1994). However, Roper (2003) demonstrated that particular nest-site characteristics influenced nesting success for real and artificial clutches, indicating that nest predation is likely not random at his study site. At this point we do not know whether nest predation on White-throated Robins at our study site can be considered random.

Another possible explanation for the lack of concordance between the outcomes for the real clutches and the artificial clutches is that predators may rarely revisit nests soon after they have depredated them. However, we found robins reusing old nests eight times during the 2002 season, in two cases within two weeks of when the previous nesting attempt failed. Hence, incentive exists for predators to revisit nests.

We assumed that nest predator communities and activity levels were approximately equivalent for the paired clutches. We feel this is a reasonable assumption given that each

artificial clutch was placed in the nest approximately one week after the real clutch had failed or produced fledglings. It is unlikely that nest predator communities and/or activity levels would have changed a great deal between the time the real clutch was present in the nest and the time the artificial clutch was present.

The modal clutch size for White-throated Robins is two and the range of clutch sizes is one to three. Some of our results compare the rates and outcomes of these clutches to the rates and outcomes for only Zebra Finch eggs (one per nest) or only quail eggs (one per nest). None of the 59 real clutches experienced partial predation, i.e., one egg or chick being lost and others surviving, indicating that predation is typically an all-or-nothing event, and that these types of comparisons are valid. The lack of partial predation in the real clutches also reinforces the idea that the finch eggs and quail eggs were differentially accessible to potential nest predators, given that partial predation did occur with these combination clutches.

Previous work investigating the correspondence of predation patterns on real and artificial clutches for two *Turdus* spp. (Cresswell 1997, Ortega *et al.* 1998) together with our results suggest that such correspondence is not easily detected. Whether this is the case because nest predation is often a random process, or because quail eggs are susceptible to a different set of nest predators than *Turdus* spp. eggs, is unclear at this point. Future studies that investigate the relationships between nest-site characteristics and the outcomes of both real and artificial clutches (e.g., Roper 2003) provide a potential method to assess the factors influencing actual predation patterns, and why artificial clutches may or may not be useful in studying these patterns. Investigating the role that parental behavior plays in nest success is also a critical issue that will influence to a great degree whether artificial clutches are useful models for natural clutches.

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