OPEN- AND CAVITY-NESTING TRAITS MERGE IN THE EVOLUTION OF AN AVIAN SUPERTRAMP, THE PEARLY-EYED THRASHER (*MARGAROPS FUSCATUS*)

Wayne J. Arendt

USDA Forest Service, International Institute of Tropical Forestry, Sabana Research Station, HC 2 Box 6205, Luquillo, PR 00773, USA. *E-mail*: warendt@fs.fed.us

Resumen. – Las características de aves que anidan en cavidades y en nidos tipo taza se combinan en la evolución del Zorzal Pardo (*Margarops fuscatus*), una especie super colonizadora . – En los aspectos temporal y quantitativo de la mayoría de los parámetros reproductivos, existe por lo general una división entre las especies de aves que utilizan nidos tipo taza y las que anidan en cavidades. Por ejemplo, parámetros como 1) iniciación, conclusión y extensión de la temporada reproductiva, 2) número de puestas por temporada, 3) extensión del período de recrudescencia y 4) la incubación y periodo de anidación, involucran periodos de tiempo más cortos en especies que anidan en tazas que en las que anidan en cavidades. Sin embargo, estos parámetros no siempre pueden compararse en especies que tienden a usar estrategias de anidación similares o mutuamente exclusivas dentro de una determinada especie. El Zorzal pardo (*Margarops fuscatus*), una especie insular que utiliza cavidades secundarias, ha adoptado varias características reproductivas de ambos grupos de aves a lo largo de su evolución, convirtiéndose en un ave super colonizadora por excelencia. Esta especie ha desarrollado habilidades de colonización superiores a las de muchas aves, como la extensión del periodo reproductivo, nidadas múltiples, eclosión asincrónica y capacidad de adaptarse rápidamente a los cambios del hábitat. El tamaño y la masa de los huevos en una misma nidada van disminuyendo luego del primero como en algunas aves no Passeriformes que anidan en cavidades, lo cual es una tendencia opuesta a la de las Passeriformes que primordialmente anidan en nidos tipo taza. Aunque el Zorzal pardo utiliza cavidades secundarias, practica la iteroparidad y ha adoptado estrategias de incubación características de especies pequeñas que anidan en tazas, acortando la duración de la etapa de incubación y permitiendo un mayor número de nidadas durante cada temporada reproductiva. Esta estrategia aumenta su fecundidad anual y finalmente su éxito reproductivo, lo cual incrementa el numero de individuos y la probabilidad de permanencia de esta especie en la región caribeña.

Abstract. – There is a dichotomy between open- and cavity-nesting species in the quantitative and temporal aspects of most reproductive parameters. For example, parameters such as 1) breeding season commencement, length, and conclusion, 2) number of clutches per season, 3) length of recrudescence periods, and 4) incubation and nestling periods, usually reflect shorter times in open nesters. However, these parameters are not always comparable among species with a proclivity for similar nest placement strategies, nor are they mutually exclusive within a given species. The Pearly-eyed Thrasher (*Margarops fuscatus*), an insular, secondary cavity nester, has adopted several reproductive traits typical of both open and cavity nesters along its evolutionary highway to becoming a premiere avian supertramp. It has evolved superior colonizing abilities, extended breeding seasons, multiple broods, rapid recycling within seasons, asynchronous hatching, and a highly adaptive resiliency to major habitat disturbances. Its egg size and mass tend to decrease with the laying of each consecutive egg within a clutch as it does in several cavity-nesting non-passerine species, which is just the opposite of the general trend found in many principally open-nesting passerines. Even though it is a secondary cavity nester, the Pearly-eyed Thrasher practices

iteroparity and has adopted other egg-laying and incubation strategies characteristic of small, open-cup nesters to minimize the duration of the egg stage, renesting more quickly with each successive clutch. It maximizes reproductive yield, and thus increases its annual fecundity and, ultimately, lifetime reproductive success, all of which enhance its numbers and chances of continual survival in the region. *Accepted 5 February 2004.*

INTRODUCTION

Birds' nests and their placement have played a central role in avian evolution, taxonomy, and systematics as well as answering some longstanding and complex questions in avian reproductive biology. Collias (1997) postulated that the diversity of nests built by passerine birds is a key to explaining their adaptive radiation during the late Tertiary. Avian systematists have used birds' nests and their placement to group various lineages within taxa (von Ihering 1904, Vaurie 1980, Winkler & Sheldon 1993, Lago-Paiva 1996). Nest structures and placement also have been used to explain the long-observed, yet often unexplained variation in several reproductive parameters such as clutch size, brood size, nest success, and iteroparity among diverse avian taxa (Nice 1957, Skutch 1967, von Berressem *et al.* 1983, Møller 1991, Martin & Li 1992, Slagsvold & Amundsen 1992, Farnsworth & Simons 2001, Tworek 2002).

The ultimate objective of any species is perpetual survival, attainable only through the constant maintenance of highly competitive, viable populations. In birds, many reproductive parameters can be altered to elevate reproductive success. However, a dichotomy often exists between the general trends of such reproductive parameters when nest placement is considered. That is, the quantitative and temporal aspects of several reproductive parameters vary greatly between nests placed in the open and those placed in protected niches, e.g., smaller clutch sizes, shorter incubation and nestling periods, but extended nesting periods with more broods per season in open nests. Species that place their open-cup nests in the surrounding vegetation are known as open-cup or simply "open" nesters, whereas species with a propensity for placing their nests (or merely eggs) within the trunks and branches of trees, or any crevice, nook, cranny, or holes in banks, etc., are generally referred to as "hole" or "cavity" nesters. They are categorized as either obligate hole nesters (all excavators, which excavate their own cavities, and several nonexcavators) or facultative hole nesters (generally nonexcavators that nest in pre-existing cavities, many of which nest in open nests as well – also termed "secondary" hole nesters, or "cavity-adopters" *sensu* Eberhard 2002). From an ecological perspective, a further distinction should be made between excavators and nonexcavators (cavity-adopters) because different suites of life-history characters are associated with these two nesting habits (Martin & Li 1992, Eberhard 2002). Herein, I compare various reproductive parameters of an insular, secondary cavity nesting Mimidae, the Pearly-eyed Thrasher (*Margarops fuscatus*) to those of both open and cavity nesters and show how the pearly-eye has incorporated traits from both modes of nest placement in its evolution of the avian supertramp reproductive strategy proposed for island birds by Diamond (1974) almost three decades ago (see also a review by Horn & Rubenstein 1986).

METHODS

This study took place in the 11,330-ha Luquillo Experimental Forest in eastern Puerto Rico (18º19'N, 65º45'W). Average annual rainfall and temperatures range, respectively, from 200 cm and 25ºC in the foothills to over 500 cm and 19ºC on peaks reaching 1075 m a.s.l. In the Holdridge life zone system, the Luquillo Experimental Forest is classified as subtropical moist to subtropical rain forest. It hosts over 240 native tree species, of which 23 are endemic. The forest is comprised of four major forest types that are altitudinally stratified and placed into separate life zones (see Ewel & Whitmore 1973 for a complete description). Located between roughly 600 and 900 m and encompassing 3318 ha (30% of the Luquillo Experimental Forest) is the palo colorado forest type in the lower montane wet forest zone. It is named for the palo colorado or swamp cyrilla (*Cyrilla racemiflora*) which, although rarely exceeding heights of 18 m, may reach almost 3 m in diameter and can survive more than 1000 years. The species' propensity for producing natural cavities makes it a preferred nest-tree for cavity-nesting birds such as the endangered Puerto Rican Parrot (*Amazona vittata*) and the Pearly-eyed Thrasher, the parrot's principal nest predator and competitor for nest sites (Snyder & Taapken 1978).

Fieldwork commenced in 1978 with the monitoring of about 40 modified wood-duck nest boxes first used as part of the Puerto Rican Parrot recovery program (Snyder *et al.* 1987). Each box was placed about 0.1 km apart at elevations ranging from about 600 to 900 m primarily in palo colorado forest. Boxes were inspected every two days, or daily during critical periods, e.g., egg laying, hatching, and the fledging of young. During the non-breeding seasons, each box was checked for signs of activity every two weeks, or weekly, just after or prior to, any given breeding season (for a more detailed description of the site and methods see Arendt 1993).

To compare the Pearly-eyed Thrasher with other open- and cavity-nesting species, a matrix of 16 life-history traits was compiled for some 1900 species worldwide and placed in Appendix 1 (available from author: wjarendt@fs.fed.us). Because so little life-history information is available for most of the included species, sample sizes for several traits, especially dispersal distances and lifetime reproductive success, are much smaller (see sample sizes in Table 1). The results that follow are derived from the comparative analyses of the matrix data. The descriptive statistics for each trait are summarized in Appendix 2 (warendt@fs.fed.us). Unless noted otherwise, all reproductive information pertaining to the Pearly-eyed Thrasher was taken from Arendt (1993).

The Kruskal-Wallis ANOVA on ranks test was used to compare statistical parameters among the four treatment groups (open nesters, primary and cavity nesters, and the Pearly-eyed Thrasher). The Mann-Whitney rank sum test was used in comparisons between the Pearly-eyed Thrasher and other members of the family Mimidae.

RESULTS

After separating primary from secondary cavity nesters, statistical comparisons were possible for 14 of the 16 life-history traits among the four treatment groups (Table 1). As anticipated, there were significant differences among 13 of the 14 comparisons between open and primary cavity nesters. Only 43% of the open- vs secondary cavity-nester comparisons were significantly different because secondary cavity nesters retain many open-cup nesting traits. Likewise, 93% of the primary cavity nester vs Pearly-eyed Thrasher comparisons and 85% of the open-nester vs thrasher comparisons were significantly different,

TABLE 1. Comparisons of selected reproductive traits among open- and cavity-nesting birds in general and the New World family Mimidae in particular, including an insular, secondary cavity-nesting mimid, the Pearly-eyed Thrasher.

Statistical parameters	Medians (25–75 percentiles)				Treatment groups*,[2]					
	Open nesters[1]	Primary cavity nesters	Secondary cavity nesters	Pearly-eyed Thrasher	OP	OS	OT	PT	ST	PS
Body mass (g)	21.0	59.7	41.1	101.0	*	*	*	*	*	
(1085[3], 473, 126, 1086)	(1.0–50.0)	(24.4–140.0)	(15.4–192.0)	(96.0–107.0)						
Egg mass (g)	2.21	5.91	2.61	8.80	*		*	*	*	*
(424, 292, 40, 2686)	(1.46–3.41)	3.17–11.90)	(1.77–4.16)	(8.30–9.20)						
Maximum clutch size[4]	4.0	4.0	5.5	3.0	*	*	*	*	*	
(696, 439, 112, 1327)	(3–5)	(3–7)	(4–7)	(2–3)						
Nestling period (days)	14.5	30.0	19.0	20.0	*	*	*	*		*
(548, 296, 99, 477)	(12–21)	(21–51)	(14.6–27)	(19–21)						
Season length (days)	150	120	150	200	*		*	*	*	*
(356, 140, 41, 19)	(120–180)	(90–150)	(120–188)	(170–226)						
Maximum lifespan (years)[4]	5	11	8	8	*	*	*	*		*
(98, 23, 22, 105)	(4–5)	(6–9)	(7–13)	(6–11)						
Average clutch size[4]	2.8	3.0	3.1	3.0	*	*	*	*		
(1089, 546, 136, 1327)	(2.0–4.0)	(2.0–4.3)	(2.0–4.5)	(2.8–3.0)						
Egg mass as % body mass[5]	11.43	7.84	11.15	7.89	*		*		*	*
(324, 230, 40, 2686)	(9.88–14.25)	(5.71–10.84)	(9.53–14.57)	(7.31–8.44)						
Average nestings/season[4]	1.8	1.0	1.0	2.3	*		*	*	*	
(350, 122, 60, 594)	(1–2)	(1–2)	(1–2)	(2–3)						
Average lifespan (years)[4]	3.5	2.7	5.9	6.0	*	*	*	*		
(20, 16, 12, 165)	(3.0–4.5)	(2.0–3.5)	(4.0–7.8)	(5.1–8.5)						
Maximum nestings/season[4]	3.0	2.0	2.0	2.8	*			*		*
(361, 117, 62, 337)	(2.0–3.0)	(2.0–3.0)	(2.0–3.0)	(2.0–3.0)						

TABLE 1. Continuation.

Statistical parameters	Medians (25–75 percentiles)				Treatment groups*[2]					
	Open nesters[1]	Primary cavity nesters	Secondary cavity nesters	Pearly-eyed Thrasher	OP	OS	OT	PT	ST	PS
Incubation period (days)	14.0	19.5	14.0	14.0	*			*		*
(578, 282, 99, 477)	(12.5–17.0)	(14.5–25.0)	(13.0–17.3)	(14.0–15.0)						
Annual adult survival	0.55	0.53	0.55	0.81[6]			*	*	*	
(92, 29, 21, 337[6])	(0.49–0.61)	(0.46–0.68)	(0.50–0.74)	(0.73–0.94)						
Fledging rate	0.54	0.63	0.48	0.41	*			*		
(114, 58, 20, 250)	(0.39–0.68)	(0.51–0.78)	(0.38–0.61)	(0.38–0.52)						

*$P < 0.05$.

[1]Includes typical open-cup and enclosed nests (e.g., globular and vaulted) not placed in holes, crevices, etc.

[2]Kruskal-Wallis one way ANOVA on ranks: OP = open vs primary cavity nesters, OS = open vs secondary cavity nesters, OT = open nesters vs Pearly-eyed Thrasher, PT = primary cavity nesters vs Pearly-eyed Thrasher, ST = secondary cavity nesters vs Pearly-eyed Thrasher, and PS = primary vs secondary cavity nesters.

[3](sample sizes for open nesters, primary and secondary cavity nesters, and the Pearly-eyed Thrasher, respectively).

[4]See Appendix 2 for descriptive statistics of parameters, including averages and maximums (available from the author: warendt@fs.fed.us).

[5]Egg mass expressed as the percentage of adult body mass.

[6]Average of 213 pearly-eyes ($\Phi = 0.85$) from a Puerto Rican rain forest (Arendt 1993) and 124 pearly-eyes ($\Phi = 0.77$) from a dry forest on the same island (Faaborg & Arendt 1995).

whereas only 54% of the secondary cavity nester vs Pearly-eyed Thrasher comparisons were significantly different because the thrasher is a secondary cavity nester. The thrasher surpassed the other three groups in 43% of the comparisons (body and egg mass, season length and average number of nestings per season, average lifespan, and annual adult survival). However, the most important finding was that when compared to the other 35 species comprising the family Mimidae, the Pearly-eyed Thrasher exceeded all others in 73% of 15 selected reproductive traits (Appendix 2). Significant differences resulted from 9 of the 14 statistical comparisons (out of 16 potential comparisons – there were insufficient sample sizes for dispersal distance and lifetime reproductive success).

DISCUSSION

Significant differences resulted in 93% and 43% of the comparisons between open- vs primary and open- vs secondary cavity-nesting species, respectively. These results mirrored those of previous studies (Moreau & Moreau 1940, Nice 1957, von Haartman 1957, Saunders *et al.* 1984, Skutch 1985, Roff 1992). However, by combining primary and secondary cavity nesters as was done in most previous studies, four parameters (season length, average number of nestings per season, average lifespan, and especially annual adult survival), which are generally shown to vary significantly between cavity and open-cup nesters, were not statistically different. One possible explanation is the fact that, historically, most comparisons of open- and cavity-nesting birds involved several small-bodied, north-temperate passerines. In the present analyses several tropical and often long-lived, large-bodied passerines and non-passerines were included, which might account for the uniformity between groups. In addition, recent investigations, many in the tropics, have shown that in the absence of heavy nest predation and brood parasitism, fledging rates for some species of open nesters can be higher than those for hole nesters (Tossas 2002). Thus, this study's higher fledging success rate of 54% for open nesters (vs 46% for some 30 species of predominantly north temperate species reviewed by Nice 1957) may have been due to the inclusion of several tropical species. In addition, several authors have undermined the long-held tenet that hole nesters are "safer" and experience higher rates of reproductive success as a result of being "sheltered" from the elements, heavy nest predation, ectoparasites, interference competition, brood parasitism, etc., (e.g., Nilsson 1984, 1986; Nilsson *et al.* 1985, Smith 1990, Pizo 1996, Christman & Dhondt 1997, Arendt 2000, Wesolowski & Stanska 2001, Miller 2002, Wesolowski *et al.* 2002; but see Albano 1992). The inclusion of several tropical and insular cavity-nesting species inhabiting highly unstable environments, as well as species that suffer from heavy brood parasitism and ectoparasites (e.g., Woodworth 1995, Arendt 2000), may explain my study's relatively lower fledging rate of 55%, which was obtained by averaging fledging rates of primary (63%) and secondary (48%) cavity nesters. A fledging rate of 55% is well below the 66% reported by Nice (1957).

The Pearly-eyed Thrasher surpassed primary and secondary cavity nesters as well as open nesters in 43% of the 14 median comparisons (body mass, egg mass, breeding season length, average number of nestings per season, annual adult survival, and average lifespan). In addition, the thrasher was comparable to secondary cavity nesters in 50% of the comparisons. Because it is a nonexcavating cavity nester, it is intuitive that the pearly-eye would measure up more closely to open and secondary cavity nesters rather than primary cavity nesters. But, how does one explain its propensity to surpass both groups

in body mass and several reproductive parameters?

Commenting on the once widely held belief that birds are prone to raise as many young as they can nourish (championed by Lack 1947–1948, and termed "the theory of maximum reproduction" by Skutch 1967), Skutch (1949, 1967, 1985) noted exceptions, especially in the more stable and wet tropics, areas in which he advocated that the rate of reproduction tends to be adjusted to the average annual mortality of individuals and nest failures, i.e., "adjusted reproduction;" see also the review by Clark & Wilson 1981 and more recent alternative arguments, which include clutch size restrictions imposed by nest predation (Martin & Clobert 1996), egg pathogens (Cook *et al.* 2003), and energetic costs in egg-laying females (Monaghan & Nager 1997, Visser & Lessells 2001, Ilmonen *et al.* 2002). Because most of the breeding biology information I used for the Pearly-eyed Thrasher came from a tropical rain forest population, one would expect this population to exhibit many reproductive traits associated with the "adjusted" reproductive strategy (Skutch 1967). For example, the adjusted reproductive strategy includes reductions in clutch size and number of broods, failure of the male to attend the nest and to form pairs, deferment of reproductive maturity, territories that limit the number of progeny reared, restriction of nesting to traditional sites, and the time-consuming construction of elaborate nests. Ironically, however, reviews of Table 1 and Appendix 2 reveal just the opposite trends in most cases for this rain forest thrasher population, but why? Although in some instances the wet tropics may be more stable, often, particularly on islands and especially in the wetter highlands, avian populations are subjected to periodic catastrophes such as severe climatic events. In such cases, Skutch (1967) argued that, as the theory of maximum reproduction predicts, each time the population is

decimated, the more prolific genotype will benefit from the advantage of rapid multiplication, and will become the "savior" of its species. This is certainly the case for the Pearly-eyed Thrasher, not only at the populational level in montane areas of Puerto Rico, but rather for the species itself throughout its range since it inhabits almost 100 Caribbean islands, most of which are subjected to severe, periodic climatic disturbances. Consequently, the most fertile Pearly-eyed Thrasher genotypes have been selected for in these ecologically stressed habitats.

The Pearly-eyed Thrasher has evolved the supertramp reproductive strategy found in island birds world-wide (Diamond 1974, 1975; Diamond & Case 1986, Arendt 1993). Caribbean mimids in general are tramp species. They constitute the only avian taxonomic group to decrease in species richness as island size increases (see Fig. 6 *in* Terborgh 1973). The thrasher has evolved superior dispersal and colonizing abilities exemplified by a well documented 175-km transmarine natal dispersal record from Barbuda to Guadeloupe (Arendt 1993). The pearly-eye is also able to recover rapidly after major habitat disturbances, only to be out competed and driven out of diverse avian communities as more competitive species recover (see examples in Arendt 1993). The pearly-eye has adopted many of the most prolific reproductive traits possible taken from both open- and cavity-nesting modes. However, the major factor governing the thrasher's persistence, wide geographical distribution, and adjustment in reproductive rates is its large body size, a trait shared by mimids in general (Murphy & Fleischer 1986). By being large the pearly-eye is at an advantage since, as Faaborg (1975) pointed out, it has a wider range of food resources available to it because it can ingest a wider range of food items of varying sizes than smaller species. This additional competitive size advantage is increased even more because

avian metabolic rates decrease on a per gram basis with increasing body size (Kendeigh 1970). For instance, although a 100-g thrasher is about three times the size of a 32-g finch, it needs only twice the daily energy intake. Thus, the thrasher has a body size and morphology that enhances its long-term survival, especially on small islands where food and other resources are often scarce such as Mona Island and several tiny cays in the Lesser Antilles inhabited by the Pearly-eyed Thrasher (Faaborg 1975, Arendt 1993). Moreover, its light clutch mass in relation to body mass puts it at a highly competitive advantage because a well-known consequence of light egg and clutch mass is a short incubation period (Lack 1968, Grant 1982), a trait shared by other large mimids (Murphy & Fleischer 1986). This preadaptation in turn increases the potential of laying more clutches each season and throughout an individual's reproductive life, thus enhancing its lifetime reproductive success. As a general rule, a 10-fold increase in body mass is associated with a 46% increase in incubation time (Rahn *et al.* 1975). Using a formula derived by Rahn *et al.* (1975), the predicted incubation period for the Pearly-eyed Thrasher would be about 20 days. Since the pearly-eye's observed incubation period is normally 14 days (with egg deposition day = 0), or almost a week shorter than predicted, one could conclude that it has reduced the incubation period to increase reproductive output. However, this hypothesis of rapid recycling as an adaptation to maximize reproductive yield would be falsified if clutch size compensated for egg size (see Smith & Fretwell 1974). In support of the notion that the pearly-eye has indeed shortened its incubation period to increase its reproductive yield rather than increase its clutch size, with the exception of one-egg clutches appearing following major habitat disturbances, its clutch size remained fairly static (modal clutch of three eggs) throughout

each season for more than 25 years (Arendt 1993). In fact, the intra-seasonal static clutch size observed in the pearly-eye is contrary to birds in general since clutch size in most species declines with each subsequent nesting (Rowe *et al.* 1994). Therefore, the rapid recycling adaptation hypothesis remains a strong contender in selecting for short incubation periods in this species. Indeed, whereas the median egg and nestling periods combined for primary cavity nesters total 50 days (Table 1), the pearly-eye is vulnerable to nest losses for only about 34 days (14-day incubation and 20-day nestling period), or about the same as the 29 days for open nesters and 33 days for secondary cavity nesters (Table 1). Therefore, contrary to its large size and propensity to nest in cavities, the pearly-eye has adopted an incubation strategy most comparable to small, open- and secondary cavity-nesting species to increase the number of clutches laid each season and, ultimately, to increase its reproductive output.

In response to periodic, major habitat disturbances (e.g., hurricanes) the Pearly-eyed Thrasher is able to compress its breeding seasons and reduce its number of nesting attempts and number of eggs laid (see Fig. 6.26A *in* Arendt 1993). Consequently, the number of hatchings, fledgings and, thus, overall reproductive success, is often higher than that experienced in non-disturbance years, a trend observed in the Puerto Rican Parrot (Meyers *et al.* 1993, Vilella & Arnizaut 1994), another cavity-nesting species inhabiting the Luquillo Experimental Forest. These two species serve as examples in addressing a recent concern (Ricklefs 2000) that the ability to increase reproductive rates and yield in response to environmental variation such as major habitat destruction has received "little rigorous quantitative scrutiny." Indeed, the concept itself, i.e., that a species is capable of evolving an adaptive response to disturbances due to the stochas-

ticity of such events, had previously been put into question (Sibly *et al.* 1991, Cooch & Ricklefs 1994). I contend that by evolving the supertramp reproductive strategy and adopting a mixture of open- and hole-nesting life-history traits, the Pearly-eyed Thrasher is preadapted in its ability to respond to periodic disturbance by adjusting its reproductive yields.

ACKNOWLEDGMENTS

REFERENCES

Albano, D. J. 1992. Nesting mortality of Carolina Chickadees breeding in natural cavities. Condor 94: 371–382.

Arendt, W. J. 1993. The Pearly-eyed Thrasher: distribution, ecology and life-history strategy of an avian supertramp. Ph.D. diss., Univ. of Wisconsin, Madison, Wisconsin.

Arendt, W. J. 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. Ornitol. Neotrop. 11: 13–63.

Christman, B. J., & A. A. Dhondt. 1997. Nest predation in Black-capped Chickadees: how safe are cavity nests? Auk 114: 769–773.

Clark, A. B., & D. S. Wilson. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. Quart. Rev. Biol. 56: 253–277.

Collias, N. E. 1997. On the origin and evolution of nest building by passerine birds. Condor 99: 252–270.

Cooch, E. G., & R. E. Ricklefs. 1994. The population consequences of life history phenomena. Quart. Rev. Biol. 29: 103–137.

Cook, M. I., S. R. Beissinger, G. A. Toranzos, R. A. Rodríguez, & W. J. Arendt. 2003. Trans-shell infection by pathogenic micro-organisms reduces the shelf life of non-incubated bird's eggs: a constraint on the onset of incubation? Proc. R. Soc. Lond. Ser. B Biol. Sci. 270: 2233–2240.

Diamond, J. M. 1974. Colonization of exploded volcanic islands by birds: the supertramp strategy. Science 184: 803–806.

Diamond, J. M. 1975. Assembly of species communities. Pp. 342–444 *in* Diamond, J. M., & M. L. Cody (eds.). Ecology and evolution of communities. Harvard Univ. Press, Cambridge, Massachusetts.

Diamond, J. M., & T. J. Case. 1986. Community ecology. Harper and Row, New York, New York.

Eberhard, J. R. 2002. Cavity adoption and the evolution of coloniality in cavity-nesting birds. Condor 104: 240–247.

Ewel, J. J., & J. L. Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. USDA Forest Service Research Paper ITF-18, Institute of Tropical Forestry, Río Piedras, Puerto Rico.

Faaborg, J. 1975. Size patterns in the structure of West Indian bird communities. Ph.D. diss., Princeton Univ., Princeton, New Jersey.

Faaborg, J., & W. J. Arendt. 1995. Survival of Puerto Rican birds: are islands really that different? Auk 112: 503–507.

Farnsworth, G. L., & T. R. Simons. 2001. How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. Auk 118: 973–982.

Grant, P. R. 1982. Variation in the size and shape of Darwin's Finch eggs. Auk 99: 15–23.

Horn, H. S., & D. I. Rubenstein. 1986. Chapter 11: Behavioral adaptations and life history. Pp. 279–300 *in* Krebs, R., & N. B. Davies (eds.). Behavioral ecology. 2nd ed. Blackwell Scientific, Oxford, UK.

Ilmonen, P., T. Taarna, & D. Hasselquist. 2002. Are incubation costs in female Pied Flycatchers expressed in humoral immune responsiveness or breeding success? Oecologia 130: 199–204.

Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of birds. Condor 72: 60–65.

Lack, D. 1947–1948. The significance of clutch size. Ibis 89: 302–352; 90: 25–45.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen & Co,. London, UK.

Lago-Paiva, C. 1996. Cavity nesting by Great Kiskadees (*Pitangus sulphuratus*): adaptation or expression of ancestral behavior? Auk 113: 953–955.

Martin, T. E., & J. Clobert. 1996. Nest predation and avian life-history evolution in Europe versus North America: A possible role of humans? Am. Nat. 147: 1028–1046.

Martin, T. E., & P. Li. 1992. Life history traits of open- vs. cavity-nesting bird. Ecology 73: 579–592.

Meyers, J. M., F. J. Vilella, & W. C. Barrow, Jr. 1993. Positive effects of Hurricane Hugo: record years for Puerto Rican Parrots nesting in the wild. Endang. Spec. Tech. Bull. 18: 1, 10.

Miller, K. E. 2002. Nesting success of the Great Crested Flycatcher in nest boxes and in tree cavities: are nest boxes safer from nest predation? Wilson Bull. 114: 179–185.

Møller, A. P. 1991. Clutch size, nest predation, and distribution of avian unequal competitors in a patchy environment. Ecology 72: 1136–1349.

Monaghan, P., & R. G. Nager. 1997. Why don't birds lay more eggs? Trends Ecol. Evol. 12: 270–274.

Moreau, R. E., & W. M. Moreau. 1940. Incubation and fledging periods of African birds. Auk 57: 313–325.

Murphy, M. T., & R. C. Fleischer. 1986. Body size, nest predation, and reproductive patterns in Brown Thrashers and other mimids. Condor 88: 446–455.

Nice, M. M. 1957. Nesting success in altricial birds. Auk 74: 305–321.

Nilsson, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand. 15: 167–175.

Nilsson, S. G. 1986. Evolution of hole-nesting in birds: on balancing selection pressures. Auk 103: 432–435.

Nilsson, S. G., C. Björkman, P. Forslund, & J. Höglund. 1985. Nesting holes and food supply in relation to forest bird densities on islands and mainland. Oecologia 66: 516–521.

Pizo, M. A. 1996. Interspecific aggression in the hole-nesting Long-tailed Tyrant, *Colonia colonus* (Aves, Tyrannidae). Cienc. Cult. (São Paulo) 48: 278–281.

Rahn, H., C. V. Paganelli, & A. Ar. 1975. Relation of avian egg weight to body weight. Auk 92: 750–765.

Ricklefs, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. Condor 102: 9–22.

Roff, D. A. 1992. The evolution of life histories. Oxford Univ. Press, New York, New York.

Rowe, L., D. Ludwig, & D. Schluter. 1994. Time, condition, and seasonal decline of avian clutch size. Am. Nat. 143: 698–722.

Saunders, D. A., G. T. Smith, & N. A. Campbell. 1984. The relationship between body weight, egg weight, incubation period, nestling period and nest site in the Psittaciformes, Falconiformes, Strigiformes and Columbiformes. Aust. J. Zool. 32: 57–65.

Sibly, R., L. Linton, & P. Calow. 1991. Testing life-cycle theory by computer simulation. II. Bet-hedging revisited. Comput. Biol. Med. 21: 357–367.

Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91: 430–455.

Skutch, A. F. 1967. Adaptive limitation of the reproductive rate of birds. Ibis 109: 579–599.

Skutch, A. F. 1985. Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. Ornithol. Monogr. 36: 575–594.

Slagsvold, T., & T. Amundsen. 1992. Do Great Tits adjust hatching spread, egg size and offspring sex ratio to changes in clutch size? J. Anim. Ecol. 61: 249–258.

Smith, L. 1990. Bees and wasps as a hazard to

hole-nesting raptors. Aust. Raptor Assoc. News 11: 12.

Smith, C. C., & S. D. Fretwell. 1974. The optimal balance between size and number of offspring. Am. Nat. 108: 499–506.

Snyder, N. F. R., & J. D. Taapken. 1978. Puerto Rican Parrots and nest predation by Pearly-eyed Thrashers. Pp. 113–120 *in* Temple, S. A. (ed.). Endangered birds, management techniques for preserving threatened species. Univ. of Wisconsin Press, Madison, Wisconsin.

Snyder, N. F. R., J. W. Wiley, & C. B. Kepler. 1987. The Parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot. Wesern Foundation of Vertebrate Zoology, Los Angeles, California.

Terborgh, J. 1973. Chance, habitat and dispersal in the distribution of birds in the West Indies. Evolution 27: 338–349.

Tossas, A. G. 2002. Puerto Rican Vireo demography in a montane habitat, with metapopulation implications. Ph. D. diss., Univ. of Puerto Rico, Río Piedras, Puerto Rico.

Tworek. S. 2002. Different bird strategies and their responses to habitat changes in an agricultural landscape. Ecol. Res. 17: 339–359.

Vaurie, C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). Bull. Am. Mus. Nat. Hist. 166: 1–357.

Vilella, F. J., & A. B. Arnizaut. 1994. Making the best of Mother Nature: managing the Puerto Rican Parrot after Hurricane Hugo. Endang. Spec. Tech. Bull. 19: 10–11.

Visser, M. E., & C. M. Lessells. 2001. The costs of egg production and incubation in great tits (*Parus Major*). Proc. R. Soc. Lond., Ser. B Biol. Sci. 268: 1271–1277.

von Berressem, K. G., H. Berressem, & K.-H. Schmidt. 1983. Comparative studies of the breeding biology of hole-nesting passerines in urban and rural habitats. J. Ornithol. 124: 431–445.

von Haartman, L. 1957. Adaptation hole-nesting birds. Evolution 11: 339–347.

von Ihering, H. 1904. The biology of Tyrannidae with respect to their systematic arrangement. Auk 21: 313–322.

Wesolowski, T., & M. Stanska. 2001. High ecto-parasite loads in hole-nesting birds – a nest box bias? J. Avian Biol. 32: 281–285.

Wesolowski, T., D. Czeszczewik, & P. Rowinski. 2002. Nest soaking in natural holes: a serious cause of breeding failure? Ornis Fenn. 79: 132–138.

Winkler, D. W., & F. H. Sheldon. 1993. Evolution of nest construction in swallows (Hirundinidae): a molecular phylogenetic perspective. Proc. Natl. Acad. Sci. USA 90: 5705–5707.

Woodworth, B. L. 1995. Ecology of the Puerto Rican Vireo and Shiny Cowbird in Guánica Forest, Puerto Rico. Ph.D. diss., Univ. of Minnesota, Minneapolis, Minnesota.