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An experimental test of the benefits of hatching asynchrony in the Rufous Hornero (*Furnarius rufus*)

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RESUMO: Um teste experimental dos benefícios de assincronia de eclosão no João-de-Barro (*Furnarius rufus*). Competição entre irmãos pode reduzir o sucesso reprodutivo dos pais e influenciar o crescimento e a sobrevivência dos filhotes. Em aves isto pode influenciar na evolução de estratégias reprodutivas, fazendo com que os pais possam controlar ou reduzir esta competição. Por exemplo, a hipótese de que hierarquia de tamanho entre os filhotes pode reduzir a competição entre irmãos e resultar em menor custo reprodutivo para os pais e aumentar a sobrevivência dos filhotes. Esta hierarquia pode ser gerada pela redução do intervalo entre a postura do ovo e o início da incubação, quando o primeiro ovo começa a ser incubado antes, ele eclode antes e os demais eclodem seguindo a ordem de postura (eclosão assíncrona). Ao contrário, quando a incubação começa apenas com a postura dos últimos ovos, a eclosão pode ser síncrona e todos os filhotes têm tamanhos aproximados (eclosão síncrona). Nós testamos esta hipótese em ninhos de João-de-Barro (*Furnarius rufus*), manipulando filhotes recentemente eclodidos, gerando dois tipos de tratamentos: ninhos com filhotes síncronos e ninhos com filhotes assíncronos. Filhotes foram movidos entre ninhos para gerar os dois tratamentos: quando a diferença entre os pesos do maior e menor filhotes era maior que 20% foram considerados ninhos assíncronos, quando a diferença era menor que 20% foram considerados síncronos. Filhotes de ninhos assíncronos cresceram mais do que filhotes de ninhos síncronos. Em ninhos assíncronos, a mortalidade ocorreu sobre os filhotes menores, em ninhos síncronos a morte foi independente do tamanho dos filhotes. Diferente do esperado a mortalidade foi menor em ninhadas síncronas. Algumas predições dos efeitos da competição entre irmãos foram suportadas neste estudo, outras não. Estudos de longo prazo podem responder melhor estas questões, especialmente em sistemas como este, onde grande variação anual no sucesso reprodutivo pode ocorrer.

PALAVRAS-CHAVE: ordem de eclosão, competição entre irmãos, sucesso reprodutivo, inanição.

ABSTRACT: Sibling competition may reduce reproductive success as well as growth and future survival of the offspring involved. In birds, this may influence the evolution of reproductive strategies concerning how adults may control or limit such competition. For example, it is hypothesized that size hierarchy in the young may reduce sibling competition and result in less costly reproduction for the parents and increased survival of the young. This hierarchy may be generated by reduction the interval between egg laying and incubation beginning with the first egg and hatching will then follow the same order as egg laying (hatching asynchrony). Conversely, when incubation begins near the last day of egg laying, hatching may be more or less synchronous and all young are the same size (hatching synchrony). We tested these hypotheses in nests of the Rufous Hornero (*Furnarius rufus*) by experimentally manipulating recently hatched young to generate two treatment types: synchronous and asynchronous nest treatments. Young were moved from one nest to another as necessary to generate the two treatments, in which a weight differential > 20% was considered asynchronous and < 20% was considered synchronous. Young from asynchronous nests grew larger than young from synchronous nests. In asynchronous nests, when mortality occurred, the smallest individuals always died, while in synchronous nests, any size was equally likely to perish. Yet, surprisingly, mortality was lower in synchronous nests, contrary to prediction. Thus, some of the predictions of sibling competition were supported in this study, while others were not. Long term studies may better answer these questions, especially in systems such as this one, where wide annual variation in reproductive success may occur.

KEY-WORDS: hatching sequence, sibling competition, reproductive success, starvation.

Hatching synchrony and asynchrony may each be beneficial for birds, depending on resource availability and environmental variability (Lack 1954, Howe 1976, Bancroft 1985, Stenning 1996, Beissinger 1996; Stoleson and Beissinger 1997, Ricklefs 1997). Synchrony is determined by when incubation begins during the process of egg laying (Ricklefs 1993, Clotfelter *et al.* 2000). If incubation begins at or near the laying of the last egg, the young will hatch synchronously. On the other hand, if incubation begins when the first egg is laid, the young

will hatch asynchronously in the sequence that the eggs were laid, leading to size difference within the clutch (Nilsson 1993, Ricklefs 1993). Thus, benefits from synchrony or asynchrony are thought to accrue due to consequences for sibling competition and reproductive success (Anderson, Reeve, and Bird 1997; Laaksonen 2004, Blanco *et al.* 2006).

Sibling competition, due to limited resources when the parents are unable to feed all the young sufficiently for their growth and survival, can reduce reproductive success due to

mortality of the weaker siblings (Ricklefs 1982; Shaanker, Ganeshaiah, and Bawa 1988; Simmons 1988). Nonetheless, rather than being a passive consequence of a size hierarchy, parent birds may compensate or favor nestlings based on the size difference (Smiseth, Lennox, and Moore 2007, Budden and Beissinger 2009). Under some conditions, however, this size hierarchy may reduce sibling competition under the peak-demand hypothesis. This hypothesis predicts that when a size difference exists, the peak energy demand of the offspring is spread out over time, such that no two offspring are at their individual peak at the same time. Thus, total demand by the offspring at any point in time is less than it would be if all offspring were of the same age (Ricklefs 1982, Magrath 1990) (Fig. 1).

We can predict that if resources are limiting during reproduction, then asynchrony may guarantee some reproductive output when food is in short supply. That is, not all young are equally affected by the lack of food and the weakest individuals die first. If the peak-demand hypothesis is correct then we expect that asynchronous clutches should have greater success than synchronous clutches. This would occur because in the asynchronous clutches the total food demand of the nest is lower than in similar sized synchronous clutches. To test these hypotheses, here we describe an experimental manipulation of hatching symmetry. We manipulate broods in a normally asynchronous bird, the Rufous Hornero (*Furnarius rufus*, Fraga 1980). Clutches are manipulated to be both synchronous and asynchronous to test the peak-demand hypothesis that when resources are limiting, asynchronous clutches avoid starvation better than synchronous clutches.

METHODS

Study Species

The Rufous Hornero (*Furnarius rufus*, Gmelin 1788, Furnariidae) is a common species in South America, whose range has expanded with agriculture in recent years (Sick 1997, Hofling and Camargo 1999). It is found from Argentina, Paraguay and Uruguay in the south, through much of Brazil south of the Amazon region (Ruschi 1979). It is monogamous and territorial (Fraga 1980). This insectivorous bird builds a complex and large mud nest in which it lays clutches from 2-5 eggs and in Argentina has been shown to have asynchronous hatching (Fraga 1980, Zyskowski and Prum 1999). Nests are found from near the ground to many meters high on horizontal branches in trees and on ledges on buildings.

Study Area

Rufous Horneros are common on the Polytechnic Center and Botanical Garden campuses of the Federal University of Paraná in the city of Curitiba, in southern Brazil (25°41'67"S, 49°13'33"W). Climate is humid subtropical without a

pronounced dry season (Maack 1981), approximately 900 m above sea level. This area has a variety of vegetation types, including patches of forest and open lawns or grasslands and with many buildings of the university. Nearby residential areas are also used by the Rufous Hornero, where they may often be seen foraging in lawns. The Hornero has become accustomed to the urban setting and is often seen feeding around restaurants and garbage cans where it consumes almost any kind of food it finds on the ground (J. J. Roper, *pers. obs.*).

Experiment

Rufous Hornero nests were found and used in the experiment in September-December 2007 and September-November 2008. Two manipulation treatments were carried out: synchronous and asynchronous. Nests were observed to determine dates of egg-laying. Based on egg-laying dates, we anticipated hatching (16-17 d, Fraga 1980) when we again checked nests to determine whether the clutch hatched synchronously. We wished to have both synchronous and asynchronous clutches, so if nests already hatched synchronously or asynchronously, they were placed in one or the other treatment. If nests were ambiguous or to provide replicas of both treatments, young birds were exchanged among nests to generate synchronous and asynchronous clutches. Hatchlings were marked by fingernail polish or by trimming a toenail so that individuals could later be recognized and thus each individual growth could be ascertained.

Nests were opened by scraping a round hole in the mud wall of the nest (as small as possible, ~ 10 cm diameter) and young birds near the time of hatching were taken out of the nests and weighed. The synchronous and asynchronous treatments were based on size differences among siblings. If the weight of the smallest sibling was $\geq 80\%$ that of the largest, the nest was considered synchronous, otherwise it was asynchronous. When nests were opened, the nestling were removed and weighed to the nearest 0.1 g when possible, or 0.5 g. If young in any nest clearly fit into a treatment (based on their weights) then that nest was included in that treatment and the opening we made was sealed. Nestlings in other nests were moved between nests to make synchronous and asynchronous clutches. In these nests, we removed the nestlings from the nest and weighed them. By choosing between individuals of different sizes in more than one nest, we chose those individuals that, when included with the nestlings already in the nest, made either synchronous or asynchronous clutches (Skagen 1987).

Just prior to the age at which nestlings normally leave the nest (> 19 days), nests were opened and the young birds were again weighed and measured. At this time, birds were banded with numbered metal bands (CEMAVE) and each individual was uniquely color-banded with plastic bands. Measurements included wing chord length, tail length, tarsometatarsal length, and bill length, width and depth.

TABLE 1: The number of *Furnarius rufus* nests, with the number of manipulated nestlings, used in the experiment to test asynchrony by year.

Year	Asynchronous			Synchronous		
	Nests	Nestlings		Nests	Nestlings	
		Total	Moved		Total	Moved
2007	4	12	5	5	14	3
2008	6	23	5	4	12	1
Total	10	35	10	9	26	4

ANALYSIS

Survival

The peak-demand hypothesis predicts that survival of the brood will be greater in asynchronous broods. Thus, we compared brood survival by treatment with a test of independence (G) in which the number of nests in each treatment were compared between survived and failed nests. Also, under this hypothesis, we expect that should mortality occur, the youngest, smallest individuals should die first. To test this, we tested for an association between birth order and survival between treatments with a test of independence (G).

Condition

The benefits that accrue to asynchrony may also be in the condition of the young at the time they leave the nest. To test for different offspring condition between the synchrony treatments, we compared the morphological measurements of the young birds at the time of final capture using the Student's t -test.

RESULTS

Egg-laying began in the first nests of the year on 16 September 2007 and 7 September 2008 and young left the last nests of this study on 10 December 2007 and 27 November 2008. Nine nests were used in 2007 and 10 nests in 2008. Of these, 10 were asynchronous and nine were synchronous, with a total of 61 nestlings (Table 1). Of those 61 nestlings, 24 died in the nest (five deaths, 19% in 2007, 19 deaths, 54% in 2008, Table 2).

TABLE 2: Comparison of mortality between treatments in the experimental analysis of hatching asynchrony in *Furnarius rufus*.

Treatment	2007		2008	
	Died	Total	Died	Total
Asynchronous	4 (33%)	12	15 (65%)	23
Synchronous	1 (7%)	14	4 (33%)	12
Mortality	19%		54%	

Mortality occurred due to starvation and was greater in 2008 ($G = 4.68$; $gl = 1$, $P < 0.05$, $n = 61$). Due to the extreme difference in mortality between years, we analyzed years separately. Mortality tended to be greatest in the asynchrony treatment in both years (minimum $G = 2.97$, $df = 1$, $P < 0.10$, Tables 2, 3).

Hatching order was associated with survival in the asynchronous treatment only and the last to hatch tended to be the ones that died in 2008 ($n = 37$, $G = 10.78$, $gl = 3$, $P < 0.05$). In synchronous nests, hatching order was unimportant for survival ($n = 26$, $G = 0.30$, $gl = 2$, $P > 0.05$, Table 3). While a greater proportion of nestlings died in the asynchrony treatment, those that survived weighed more than nestlings in the synchrony treatment (one-tailed $t = 1.83$, $gl = 32$, $P < 0.05$, Fig. 2).

DISCUSSION

While generally, *Furnarius rufus* is described as having asynchronous hatching (Fraga 1980), in Curitiba, natural nests varied from synchronous to asynchronous. This may occur in other species as well (Clark and Wilson 1981; Slagsvold 1985, 1986a; Harper *et al.* 1992, 1993), and may indicate adaptive changes to environmental conditions (Lack 1947) or may indicate that control of hatching sequence is not possible (Harper *et al.* 1994). Here we find equivocal evidence of the importance of asynchrony and which may be a consequence of rapid range expansion of the Rufous Hornero.

Current distribution of *Furnarius rufus* is due to rapid range expansion that followed after a large area of Brazil was deforested, such as the state of Paraná. In the new habitats, it is quite possible that the original advantages of hatching asynchrony are no longer applicable. In less extreme climate, such as Curitiba as compared with the original range of the species, perhaps food availability is more constant. Also, perhaps urban settings, with the many anthropic sources of water, food and

TABLE 3: Birth order and mortality in experimental manipulation of hatching asynchrony in *Furnarius rufus*.

Hatching order	2007				2008			
	Asynchronous		Synchronous		Asynchronous		Synchronous	
	Died	Total	Died	Total	Died	Total	Died	Total
1	1	4	2	5	1	6	1	4
2	2	4	1	5	3	6	1	4
3	1	4	0	4	6	6	2	4
4					5	5		
Total	4	12	3	14	15	23	4	12

nesting locations have together reduced the benefits of asynchrony. However, the question arises as to whether variation in synchrony is also found in its original range.

We originally hypothesized that in the species' original range, asynchrony was a consequence of their nest type. That is, the large, oven shaped nest built on branches exposed to the sun may act as incubation chambers and the heat induce development in the eggs prior to incubation by the parent birds. If parent birds only begin incubation on the penultimate egg, as is common in synchronous species, and the nest acted as an incubation chamber, hatching asynchrony would occur whenever temperatures were adequate. Thus, asynchrony in its original range would not be a consequence of behavior, but rather would be due to the nest and the climate. Once reaching new environments, asynchrony should disappear if the temperature is not high enough and incubation initiates development. Unfortunately, during our second field season, mortality on juvenile birds was extremely high (> 50%) and seemed to be dissociated from hatching patterns.

Due to high mortality rates, we could find no clear evidence for benefit nor cost due to asynchrony. We predicted that the peak demand hypothesis would be found correct, in which the size hierarchy reduces sibling competition and increases overall clutch survival (Ricklefs 1965; Parsons 1975; Zach 1982; Husel 1985; Stockland and Amundsen 1988, Cotton *et al.* 1999; Clotfelter *et al.* 2000). However, here, a trend seemed to suggest that the youngest nestlings had the greatest mortality. Also, the surviving young from the asynchronous clutches seemed to fledge at a slightly greater weight, which might indicate that once the clutch size was reduced, the

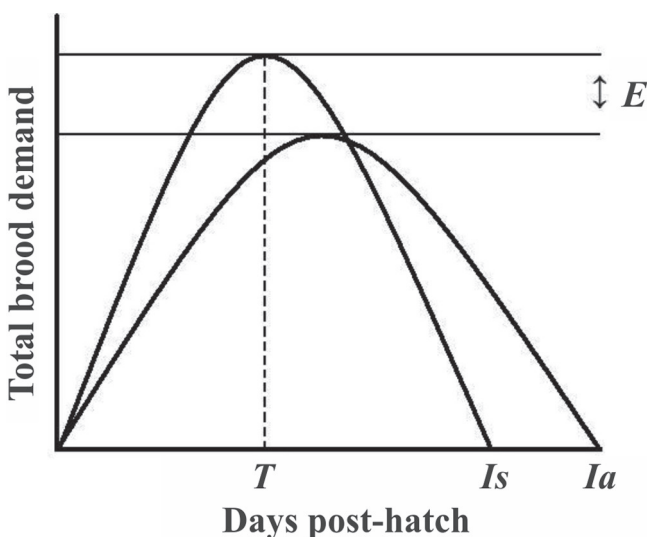


FIGURE 1: Hypothetical model of the importance of hatching asynchrony under the peak demand hypothesis. The peak energy demand for an individual nestling occurs at age (T). The reduction in peak load is represented by (E). Peak demand is at the horizontal tangent to the curve and I_A indicates asynchrony and I_S synchrony. Thus, when all young reach their growth curve maxima in synchrony, their combined demand for food reaches a higher peak. For asynchronous clutches, on the other hand, growth peaks are spread out over time and the maximum is lower than for synchronous clutches (following Wiebe and Bortolotti 1994).

largest (oldest) nestling was then freed from competition and could grow more rapidly (Fig. 2). In some species, early size differential is great, but it gradually declines with nestling age (Zach 1982; Clotfelter *et al.* 2000).

The surprisingly large mortality rate of nestlings in 2008 probably has important consequences for how we think of asynchrony. For example, if mortality is occasionally very high and irrespective of hatching synchrony, does it then mask the possible benefits of asynchrony in other years? The increased weight in surviving asynchronous nestlings suggests a possible benefit to asynchrony, especially in stressful years. In asynchronous clutches, in normal years, perhaps the peak demand hypothesis (Husel 1972; Walsberg 1983) is valid and the size hierarchy may help in brood survival (Lack 1954; O'Connor 1978; Zach 1982; Bortolotti 1989). On the other hand, when food is limiting, either the large young benefit to the detriment of the small (Skagen 1987; Cotton *et al.* 1999; Clotfelter *et al.* 2000), or, for every nestling that dies, the larger remaining nestlings will then get a larger total proportion of the food delivered by the parents. In the former case, the young may survive but fledge in poorer condition, while in the latter case, the few young that survive do so in much better condition. If so, this suggests a previously unrecognized possible benefit to hatching asynchrony. Also, considering the impact of occasional years with extremely high mortality, we need to examine costs and benefits to hatching synchrony over a longer term and we should include subsequent survival of the young to determine whether the potential benefit of heavier survivors in asynchronous nests translates into future reproductive success.

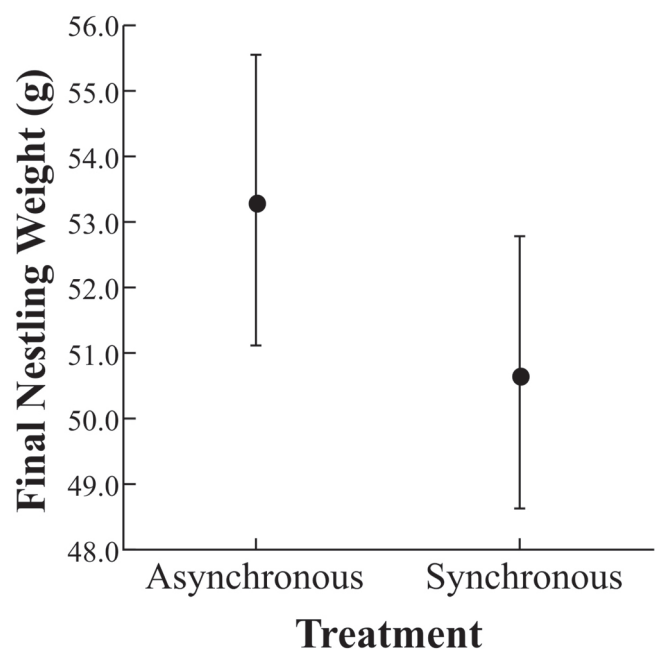


FIGURE 2: Comparison of weights of nestlings near the time at which they leave the nest in the two asynchrony treatments. Nestlings in asynchronous nests were heavier (one-tailed $t = 1.83$, $gl = 32$, $P < 0.05$).

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LITERATURE CITED

- Anderson, D. J.; Reeve, J. and Bird, D. M. (1997).** Sexually dimorphic eggs, nestling growth and sibling competition. *Functional Ecology*, 11:331-335.
- Bancroft, G. T. (1985).** The Influence of Total Nest Failures and Partial Losses on the Evolution of Asynchronous Hatching. *The American Naturalist*, 126:495-504.
- Beissinger, S. R. (1996).** On the limited breeding opportunities hypothesis for avian clutch size. *The American Naturalist*, 147:655-658.
- Blanco, G.; Frias, O.; Martínez, J.; Lemus, J. A.; Merino, R. and Jiménez, B. (2006).** Sex and rank in competitive brood hierarchies influence stress levels in nestlings of a sexually dimorphic bird. *Biological journal of the Linnean Society*, 88:383-390.
- Bortolotti, G. R. (1989).** Factors influencing the growth of Bald Eagles in north central Saskatchewan. *Canadian Journal of Zoology*, 67:606-611.
- Budden, A. E. and Beissinger, S. R. (2009).** Resource allocation varies with parental sex and brood size in the asynchronously hatching green-rumped parrotlet (*Forpus passerinus*). *Behavioral Ecology and Sociobiology*, 63:637-647.
- Clark, A. B. and Wilson, D. S. (1981).** Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Quarterly Review of Biology*, 56:253-277.
- Clotfelter, E. D.; Whittingham, L. A. and Dunn, P. O. (2000).** Laying order, hatching asynchrony and nestling body mass in Tree Swallows *Tachycineta bicolor*. *Journal of Avian Biology*, 31:329-334.
- Cotton, P. A.; Wright, J. and Kacelnik, A. (1999).** Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *The American Naturalist*, 153:412-420.
- Fraga, R. M. (1980).** The breeding of Rufous Horneros (*Furnarius rufus*). *Condor*, 82:58-68.
- Harper, R. G.; Juliano, S. A. and Thompson, C. F. (1992).** Hatching asynchrony in the House Wren: A test of the brood-reduction hypothesis. *Behavioral Ecology and Sociobiology*, 3:76-83.
- Harper, R. G.; Juliano, S. A. and Thompson, C. F. (1993).** Avian hatching asynchrony: Brood classification based on discriminant function analysis of nestling masses. *Ecology*, 74:1191-1196.
- Harper, R. G.; Juliano, S. A. and Thompson, C. F. (1994).** Intrapopulation variation in hatching synchrony in House Wrens: test of the individual-optimization hypothesis. *The Auk*, 111(3):76-83.
- Hoffling, E. and Camargo, H. F. A. (1999).** *Aves no Campus da Cidade Universitária Armando Salles Oliveira*. São Paulo: Edusp, 126 p.
- Howe, H. F. (1976).** Egg size, hatching asynchrony, sex, and brood reduction in the Common Grackle. *Ecology*, 57:1195-1207.
- Hussell, D. J. T. (1972).** Factors affecting clutch size in Artic passerines. *Ecological Monographs*, 42:317-364.
- Hussell, D. J. T. (1985).** On the adaptive basis for hatching asynchrony: Brood reduction, nest failure and asynchronous hatching in Snow Buntings. *Ornis Scandinavica*, 16:205-212.
- Laaksonen, T. (2004).** Hatching asynchrony as a bet-hedging strategy – an offspring diversity hypothesis. *Oikos*, 104:616-620.
- Lack, D. (1947).** The significance of clutch size. *Ibis*, 89:302-352.
- Lack, D. (1954).** The natural regulation of animal numbers. Clarendon Press, Oxford.
- Maack, R. (1981).** Geografia física do estado do Paraná. Rio de Janeiro, RJ.
- Magrath, R. M. (1990).** Hatching asynchrony in altricial birds. *Biological Reviews*, 65:587-622.
- Nilsson, J. A. (1993).** Energetic constraints on hatching asynchrony. *The American Naturalist*, 141:158-166.
- O'Connor, R. J. (1978).** Brood reduction in birds: selection for fratricide, infanticide and suicide? *Animal Behaviour*, 26:79-96.
- Parsons, J. (1975).** Asynchronous hatching and chick mortality in the Herring Gull *Larus argentatus*. *Ibis*, 117:517-520.
- Ricklefs, R. E. (1965).** Brood reduction in the Curve-billed Thrasher. *Condor*, 67:505-510.
- Ricklefs, R. E. (1982).** Some considerations on sibling competition and avian growth rates. *The Auk*, 99:141-147.
- Ricklefs, R. E. (1993).** Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. *Current Ornithology*, 11:199-276.
- Ricklefs, R. E. (1997).** Comparative demography of new world populations of thrushes (*Turdus* spp.). *Ecological Monographs*, Vol. 67, No. 1, pp. 23-43.
- Ruschi, A. (1979).** *Aves do Brasil*. Ed. Rios. São Paulo, SP.
- Shaanker, U. R.; Ganeshaiah, K. N. and Bawa, K. S. (1988).** Parent-offspring conflict, sibling rivalry and brood size reduction in plants. *Annual Review of Ecology and Systematics*, 19:177-205.
- Sick, H. (1997).** *Ornitologia Brasileira*. Ed. Nova Fronteira. Rio de Janeiro, RJ.
- Simmons, R. E. (1988)** Offspring quality and the evolution of cainism. *Ibis*, 130:339-357.
- Skagen, S. K. (1987).** Hatching asynchrony in American Goldfinches: an experimental study. *Ecology*, 68(6):1747-1759.
- Slagsvold, T. (1985).** Asynchronous hatching in passerine birds: Influence of hatching failure and brood reduction. *Ornis Scandinavica*, 16:81-87.
- Slagsvold, T. (1986).** Hatching asynchrony: Inter-specific comparisons of altricial birds. *The American Naturalist*, 128:120-125.
- Smiseth, P. T.; Lennox, L. and Moore, A. J. (2007).** Interaction between parental care and sibling competition: parents enhance offspring growth and exacerbate sibling competition. *Evolution*, 61:2331-2339.
- Stenning, M. J. (1996).** Hatching asynchrony, brood reduction and other rapidly reproduction hypotheses. *Trends Ecology Evolution*, 11:243-246.
- Stockland, J. N. and Amundsen, T. (1988).** Initial size hierarchy in broods of the Shag: relative significance of egg size and hatching asynchrony. *Auk*, 105:308-315.
- Stoleson, S. H. and Beissinger, S. R. (1997).** Extreme hatching asynchrony, brood reduction, and food limitation in a Neotropical parrot: an experimental study. *Ecological Monographs*, 67:131-154.
- Walsberg, G. E. (1983).** Avian ecological energetics. Pages 161-220 in D. S. Farner and J. R. King, editors. *Avian biology*. Academic Press, New York, USA.
- Zach, R. (1982).** Hatching asynchrony, egg size, growth, and fledging in Tree Swallows. *Auk*, 99:695-700.
- Zyskowski, K. and Prum, R. O. (1999).** Phylogenetic analysis of the nest architecture of Neotropical ovenbirds (Furnariidae). *The Auk*, 116(4):891-911.