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Influência de pistas olfativas, visuais e da ejeção de ovos na taxa de predação de ninhos

PAULO VICTOR RESENDE DOS SANTOS

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INFLUÊNCIA DE PISTAS OLFATIVAS, VISUAIS E DA EJEÇÃO DE OVOS NA TAXA DE PREDAÇÃO DE NINHOS

PAULO VICTOR RESENDE DOS SANTOS

Dissertação de mestrado apresentada ao Programa de Pós-Graduação em Ecologia da Universidade de Brasília como requisito parcial para obtenção do título de mestre em Ecologia

Orientador: Prof. Dr. Eduardo Bessa

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DEDICATÓRIA

Na esperança de um dia ver o conhecimento científico a serviço do povo e os muros da universidade não mais como muralhas, dedico esse trabalho a todas/os aqueles que acreditam na educação como potencial de transformação e um mundo mais justo e igualitário.

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INTRODUÇÃO GERAL

Parasitismo de ninhada

O investimento parental é todo esforço realizado pelos parentais que aumente a sobrevivência de seus filhotes, mas que em troca diminua suas oportunidades de reprodução no futuro (Trivers, 1972). Tais esforços muitas vezes demandam alto custo energético aos parentais, o que torna comum o desenvolvimento de mecanismos que visam burlar tais custos, como o parasitismo de ninhada (Stevens, 2013). Presente em grupos como peixes (Sato, 1986; Stauffer-Jr et al., 2010), insetos (Dapporto et al., 2004) e, mais comumente, aves (Rothstein, 1971, 1975; Davies & Brooke, 1989; Lyon, 2003), o parasitismo de ninhada pode ser definido como a postura de ovos em um ninho onde os filhotes não apresentam qualquer relação de parentesco genético com seus parentais sociais. Esse comportamento pode ser facultativo, quando fêmeas podem construir ninhos e criar seus próprios filhotes, mas optam por colocar seus ovos no ninho de outra fêmea (Weller, 1959; Croston & Hauber, 2010), ou obrigatório, quando fêmeas não possuem tal capacidade e então colocam ovos no ninho de outro indivíduo se livrando dos custos de criar seus próprios filhotes (Rothstein, 1990). Tal mecanismo ainda pode ocorrer entre indivíduos da mesma espécie (parasitismo intraespecífico) (Carvalho et al., 2006; Davanço et al., 2012) ou de espécies diferentes (parasitismo interespecífico) (Lanyon, 1992; Hauber 2003).

O parasitismo intraespecífico é comumente encontrado em aves precociais e pode ser explicado por altas proporções de fêmeas não pareadas em uma população, escassez de locais para a construção de ninhos e fêmeas que perderam seus ninhos por atividades antrópicas ou naturais (Yom-Tov, 1980). Por outro lado, o parasitismo interespecífico é comum em aves altriciais. Acredita-se que o mesmo tenha evoluído ao menos sete vezes em sete táxons diferentes de forma independente, a partir de um ancestral com cuidado parental e como uma consequência evolutiva de mudanças ecológicas em atributos como dieta, migração e alcance no padrão reprodutivo da espécie, tendo como resultado a redução nos custos de sua reprodução (Krüger & Davies, 2002; Sorenson & Payne, 2002; Krüger, 2007). Dois dos principais representantes do parasitismo interespecífico em aves são as espécies *Cuculus canorus* e *Molothrus bonariensis*, ambos parasitas obrigatórios, conhecidos por parasitar mais de 100 espécies diferentes de hospedeiros (Soler et al., 1999).

Essa relação parasita-hospedeiro tem sido responsável pela coevolução de estratégias que já foram demonstradas em vários estudos (Payne, 1977; Davies & Brooke, 1989; Payne, 1998). Enquanto parasitas economizam a energia que seria gasta na incubação dos ovos e alimentação de seus filhotes, investindo a mesma na produção de ninhadas maiores (Croston & Hauber, 2010), hospedeiros precisam evitar que seus ninhos sejam parasitados e desenvolver estratégias adicionais para se livrar de tais custos caso o parasitismo ocorra. Essa corrida armamentista pode ser exemplificada por parte do parasita através da hipótese da máfia (Hoover & Robinson, 2007) e o mimetismo de ovos e filhotes do hospedeiro (Langmore et al., 2011; Moskát et al., 2012). Os hospedeiros, por sua vez, podem defender seus ninhos por meio de comportamentos agonísticos e "*mobbing*" (Marchetti, 1992; Soler, 2013), abandonar suas ninhadas quando sofrem parasitismo (Hosoi & Rothstein, 2000), reconhecer e ejetar ovos do parasita (Bolen et al., 2000; Fleischer & Woolfenden, 2004; Peer et al., 2007; Segura et al., 2016) e ainda relocar os ovos do parasita para regiões periféricas do ninho ou reduzir as taxas de cuidado parental para os filhotes parasitas (Lyon, 2003).

Entretanto, mesmo desenvolvendo a capacidade de reconhecer e ejetar ovos do parasita, alguns estudos mostram que os hospedeiros não o fazem (Antonov et al., 2007, 2009; Soler et al., 2012). Tal decisão pode estar relacionada ao fato de que um dos principais custos associados à ejeção de ovos é a falha no reconhecimento do ovo parasita e ejeção de ovos da própria ninhada. Essa estratégia ocorre tanto pela dificuldade em lidar com ovos miméticos quanto por limitações morfológicas, *e.g.* tamanho do bico, que impedem que aves com bico pequeno sejam capazes de manusear com eficiência ovos do parasita e então aceitam tais ovos visto que para essas espécies a ejeção apresenta um custo muito alto (Davies & Brooke, 1989; Moksnes et al., 1991; Peer & Sealy, 2004).

Ademais, outro custo associado à ejeção de ovos seria o aumento na taxa de predação de ninhos. Ovos ejetados podem deixar pistas olfativas/visuais que acabam por atrair mais predadores ao ninho e podem comprometer toda a ninhada (Weller, 1959; De Mársico et al., 2016). Assim, para que a ejeção de ovos ocorra é necessário que seus benefícios sejam maiores que seus custos. Isso faz com que em muitos casos a não ejeção de ovos do parasita se torne uma lacuna no conhecimento, principalmente por não sabermos quais atributos da história de vida de cada hospedeiro são os responsáveis por essa tomada de decisão e em quais situações a ejeção de ovos se torna desejável e em quais não.

Predação de ninhos

O sucesso reprodutivo de um indivíduo pode ser definido pelo número de descendentes que ele consegue produzir em uma estação reprodutiva. Em aves, esse sucesso é medido principalmente pelo número de filhotes que sobrevivem até a independência, uma vez que é inviável acompanhar indivíduos até sua fase adulta e/ou reprodutiva (Major & Kendall, 1996). Entretanto, para garantir a sobrevivência de seus filhotes, parentais precisam lidar com fatores como o parasitismo de ninhada (Davies & Brooke, 1989), condições temporais extremas (Wingfield, 1984; Wingfield et al., 1999), fragmentação de habitats (Gibbs, 1991; Robinson et al., 1995) e a predação de ninhos e filhotes, que atualmente é uma das maiores causas do insucesso reprodutivo das ninhadas (Ricklefs, 1969; Martin, 1993; Donald et al., 2002; Thompson III, 2007). Em alguns casos a predação de ninhos pode ser responsável por até 80% da taxa de mortalidade de ninhegos (Martin, 1993; Donald et al., 2012).

A predação de ninhos pode resultar em diversos custos reprodutivos para suas presas (Magnhagen, 1991). Em risco iminente de predação de ninhos, machos e fêmeas podem reduzir suas taxas de display sexual, deslocando suas preferências sexuais para parceiros menores e menos atrativos, resultando em menores taxas de cópulas como foi observado na espécie *Syngnathus typhle* que apresenta reversão de papéis sexuais (Berglund, 1993; Sih, 1994). Outro efeito negativo causado pelo risco de predação é o stress crônico. Estudos com as espécies *Saxicola torquata* (Cartaxo-comum) e *Hirundo rustica* (Andorinha do pescoço vermelho) mostraram que o aumento no risco de predação levou as espécies a uma produção elevada de hormônios corticosteroides e que isso pode ser responsável por falhas nas funções reprodutivas, queda no sistema imune, morte de células neuronais e perda de proteínas que resultam em menores tamanhos corporais (Scheuerlein et al., 2001; Vitousek et al., 2014). Além disso, fêmeas grávidas ou incubando ovos muitas vezes apresentam menor mobilidade, são mais conspícuas a predadores ou possuem menores taxas de escape do que fêmeas não grávidas, sendo então passíveis de sofrerem maiores taxas de predação (Magnhagen, 1991).

Por outro lado, parentais também podem desenvolver estratégias anti-predatórias. Em elevado risco de predação aves podem alterar a escolha do sítio de nidificação para locais mais protegidos (Eggers et al., 2006), utilizar diferentes materiais na construção de seus ninhos buscando evitar a conspicuidade dos mesmos a predadores visuais (Møller, 1987), realizar comportamentos como o *"nest sanitation"* eliminando pistas que podem atrair predadores ao ninho (Ibáñez-Álamo et al., 2013, 2016) e ainda exibir displays de distração (Scheuerlein et al., 2001). Portanto, muitos mecanismos reprodutivos, comportamentais e atributos da história de vida exibidas pelos parentais podem ser uma resposta às forças evolutivas impostas pela predação de ninhos (Martin et al., 2000; Scheuerlein et al., 2001).

Nos trópicos a predação de ninhos parece ser ainda mais acentuada. Quando comparadas a regiões temperadas, maiores taxas de predação de ninhos podem ser resultado da maior riqueza de espécies e maior taxa de interações bióticas nos trópicos (Schemske et al., 2009). Como resultado, estudos sugerem que a presença de ninhadas menores, maiores taxas de cuidado parental e menores quantidades de ninhadas por ano, tipicamente encontrada em aves nos trópicos, resultam da elevada taxa de predação encontrada nessa região (Scheuerlein et al., 2001; Eggers et al., 2006). Entretanto, essa relação parece ser bem variável ao passo que outros estudos encontram resultados opostos (Oniki, 1979; Soderström, 1999; Martin et al., 2000). Sendo assim, fica cada vez mais evidente a necessidade de estudos sobre predação de ninhos nos trópicos, além de estudos que identifiquem quem são os predadores presentes nessas áreas, quais as principais pistas que estão sendo utilizadas por esses predadores para achar suas presas e quais estratégias antipredação estão sendo exibidas pelos parentais para se livrar de tal custo.

Tendo em vista o contexto apresentado, em minha dissertação trago um recorte sobre a utilização de pistas visuais e olfativas e sua influência na predação de ninhos artificiais em um fragmento do Cerrado no Brasil central. Em meu primeiro capítulo busco fazer uma intersecção entre o parasitismo de ninhada e a predação de ninhos, discutindo quais os custos que a ejeção de um ovo pode apresentar aos hospedeiros. Ainda, busco identificar quais pistas do ovo ejetado (olfativas e/ou visuais) estão relacionadas a maiores taxas de predação de ninhos, entendendo qual a principal forma sensorial de orientação, que predadores nessa área estão utilizando para encontrar suas presas. Em meu segundo capítulo busco preencher uma lacuna do primeiro estudo, tentando entender se pistas visuais são determinantes para a maior taxa de predação de ninhos nessa área. Trago ainda um paralelo sobre as implicações que a presença de parentais e a coloração conspícua de um indivíduo pode apresentar aos ovos e filhotes remanescentes de uma ninhada.

REFERÊNCIAS

Antonov, A., Stokke, B. G., Moksnes, A., & Roskaft, E. (2007). Getting rid of the cuckoo *Cuculus canorus* egg: why do hosts delay rejection?. *Behavioral Ecology*, 19, 100-107. https://doi.org/10.1093/beheco/arm102

Antonov, A., Stokke, B. G., Moksnes, A., & Roskaft, E. (2009). Evidence for egg discrimination preceding failed rejection attempts in a small cuckoo host. *Biology Letters*, 5, 169-171. https://doi.org/10.1098/rsbl.2008.0645

Berglund, A. (1993). Risky sex: male pipefishes mate at random in the presence of a predator. *Animal Behaviour*, 46, 169-175. https://doi.org/10.1006/anbe.1993.1172

Bolen, G., Rothstein S. I., & Trost, C. H. (2000). Egg recognition in yellow-billed and black-billed magpies in the absence of interspecific parasitism: implications of parasite-host coevolution. *The Condor*, 102, 432-438. https://doi.org/10.1650/0010-5422(2000)102[0432:ERIYBA]2.0.CO;2

Carvalho, C. B. V., Macedo, R. H., & Graves, J. A. (2006). Breeding strategies of a socially monogamous neotropical passerine: Extra-pair fertilizations, behavior, and morphology. *The Condor*, 108, 579-590. https://doi.org/10.1650/0010-5422(2016)108[579:BSOASM]2.0.CO;2

Croston, R., & Hauber, M. (2010). The ecology of avian brood parasitism. *Nature Education Knowledge*, 3, 56.

Dapporto, L., Cervo, R., Sledge, M. F., & Turillazzi, S. (2004). Rank integration in dominance hierarchies of host colonies by the paper wasp social parasite *Polistes sulcifer* (Hymenoptera, Vespidae). *Journal of Insect Physiology*, 50, 217-223. https://doi.org/10.1016/j.jinsphys.2003.11.012

Davanço, P. V., Souza, L. M., de Oliveira, L. S., & Francisco, M. R. (2012). Intraspecific brood parasitism of the Pale-breasted Thrush (*Turdus leucomelas*). *The Wilson Journal of Ornithology*, 124, 611-614. https://doi.org/10.2307/23324571

Davies, N., & Brooke, M. D. L. (1989). An experimental study of co-evolution between the cuckoo, Cuculus canorus, and its hosts. I. Host egg discrimination. *The Journal of Animal Ecology*, 58, 207-224. https://doi.org/10.2307/4995

De Mársico, M. C., Ursino, C. A., & Reboreda, J. C. (2016). Experimental evidence for an antipredatory function of egg rejection behaviour in a common host of the brood-parasitic shiny cowbird. *Behavioral Ecology and Sociobiology*, 70, 1689-1697. https://doi.org/10.1007/s00265-016-2174-3

Donald, P. F., Evans, A. D., Muirhead, L. B., Buckingham, D. L., Kirby, W. B., & Schmitt, S. I. A. (2002). Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis*, 144, 652-664. https://doi.org/10.1046/j.1474-919X.2002.00101.x

Eggers, S., Griesser, M., Nystrand, M., & Ekman, J. (2006). Predation risk induces changes in nest-site selection and clutch size in the Siberian Jay. *Proceedings of the Royal Society of London B: Biological Sciences*, 273, 701-706. https://doi.org/10.1098/rspb.2005.3373

Fleischer, T. L., & Woolfenden, G. E. (2004). Florida scrub-Jays eject foreign eggs added to their nests. *Journal of Field Ornitholgy*, 75, 49-50. https://doi.org/10.1648/0273-8570-751.49

Gibbs, J. P. (1991). Avian Nest predation in tropical wet forest: an experimental study. *Oikos*, 60, 155-161. https://doi.org/10.2307/3544861

Hauber, M. E. (2003). Interspecific brood parasitism and the evolution of host clutch sizes. *Evolutionary Ecology Research*, 5, 559-570.

Hoover, J. P., & Robinson, S. K. (2007). Retaliatory mafia behaviour by a parasitic cowbird favors host acceptance of parasitic eggs. *Proceedings of the National Academy of Sciences*, 104, 4479-4483. https://doi.org/10.1073/pnas.0609710104

Hosoi, S. A., & Rothstein, S. I. (2000). Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Animal Behaviour*, 59, 823-840. https://doi.org/10.1006/anbe.1998.1370

Krüger, O., & Davies, N. B. (2002). The evolution of cuckoo parasitism: a comparative analysis. *Proceedings of the Royal Society of London B: Biological Sciences*, 269, 375-381. https://doi.org/10.1098/rspb.2001.1887

Krüger, O. (2007). Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Philosophical Transactions of the Royal Society of London B*, 362, 1873-1886. https://doi.org/10.1098/rstb.2006.1849

Ibáñez-Álamo, J. D., Sanllorente, O., Arco, L., & Soler, M. (2013). Does nest predation risk induce parent birds to eat nestlings' fecal sacs? An experimental study. *Annales Zoologici Fennici*, 50, 71-78. https://doi.org/10.5735/086.050.0106

Ibáñez-Álamo, J. D., Ruiz-Raya, F., Rodriguez, L., & Soler, M. (2016). Fecal sacs attract insects to the nest and provoke an activation of the immune system of nestlings. *Frontiers in Zoology*, 2016, 13:3. https://doi.org/10.1186//s12893-016-0135-3

Langmore, N. E., Stevens, M., Maurer, G., Heinsohn, R., Hall, M. L., Peters, A., & Kilner, R. M. (2011). Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society of London B: Biological Sciences*, 278, 2455-2463. https://doi.org/10.1098/rspb.2010.2391

Lanyon, S. M. (1992). Interspecific brood parasitism in blackbirds (Icterinae): A phylogenetic perspective. *Science*, 255, 77-79. https://doi.org/10.1126/science.1553533

Lyon, B. E. (2003). Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature*, 422, 495-499. https://doi.org/10.1038/nature01505

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6, 183-186. https://doi.org/10.1016/0169-5347(91)90210-O

Major, R. E., & Kendal, C. E. (1996). The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, 138, 298-307. https://doi.org/10.1111/j.1474-919X.1996.tb04342.x

Marchetti, K. (1992). Cost to host defence and the persistence of parasitic cuckoos. *Proceedings of the Royal Society of London B: Biological Sciences,* 248, 41-45. https://doi.org/10.1098/rspb.1992.0040

Martin, T. E. (1993). Nest predation and nest sites: new perspectives on old patterns. *BioScience*, 43, 523-532. https://doi.org/10.2307/1311947

Martin, T. E., Martin, P. R., Olson, C. R., Heidinger, B. J., & Fontiane, J. J. (2000). Parental care and clutch size in North and South American Birds. *Science*, 287, 1482-1485. https://doi.org/10.1126/science.287.5457.1482

Moksnes, A., Roskaft E., & Braa, A. T. (1991). Rejection Behavior by common cuckoo hosts towards artificial brood parasite eggs. *The Auk*, 108, 348-354.

Moskát, C., Takasu, F., Muñoz, R., Nakamura, H., Bán, M., & Barta, Z. (2012). Cuckoo parasitism in two closey-related Acrocephalus warblers in distant areas: a case of parallel coevolution?. *Chinese Birds*, 3, 320-329. https://doi.org/10.5122/cbirds.2012.0038

Møller, A. P. (1987). Egg predation as a selective factor for nest design: an experiment. *Oikos*, 50, 91-94. https://doi.org/10.2307/3565404

Oniki, Y. (1979). Is nesting success of birds low in the tropics?. *Biotropica*, 11, 60-69. https://doi.org/10.2307/2388174

Payne, R. B. (1977). The ecology of brood parasitism in birds. *Annual Review of Ecology and Systematics*, 8, 1-28. https://doi.org/10.1146/annurev.es.08.110177.000245

Payne, R. B. (1998). Brood parasitism in birds: strangers in the nest. *BioScience*, 48, 377-386. https://doi.org/10.2307/1313376

Peer, B. D., & Sealy, S. G. (2004). Correlates of egg rejection in hosts of the brown-headed cowbird. *The Condor*, 106, 580-599. https://dx.doi.org/10.1650/7412

Peer, B. D., Rothstein, S. I., Delaney, K. S., & Fleischer, R. C. (2007). Defence behavior against brood parasitism is deeply rooted in mainland and island scrub-jays. *Animal Behaviour*, 73, 55-63. https://doi.org/10.1016/j.anbehav.2006.06.005

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, 1-48. https://doi.org/10.5479/si.00810282.9

Rothstein, S. I. (1971). An experimental and teleonomic investigation of avian brood parasitism. *The Condor*, 77, 250-271. https://doi.org/10.2307/1366221

Rothstein, S. I. (1975). Evolutionary rates and host defenses against avian brood parasitism. *The American Naturalist*, 109, 161-176. https://doi.org/10.1086/282984

Rothstein, S. I. (1990). A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics*, 21, 481-508. https://doi.org/10.1146/annurev.es.21.110190.002405

Robinson, S. K., Thompson III, F. R., Donovan, T. M., Whitehead, D. R., & Faaborg, J. (1995). Regional forest fragmentation and nesting success of migratory birds. *Science*, 267, 1987-1990. https://doi.org/10.1126/science.267.5206.1987

Sato, T. (1986). A brood parasitic catfish of mouthbrooding cichlid fishes in lake Tanganyika. *Nature*, 323, 58-59. https://doi.org/10.1146/annurev.es.21.110190.002405

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions?. *Annual Review of Ecology, Evolution and Systematics*, 40, 245-269. https://doi.org/10.1146/annurev.ecolsys.39.110707.173430

Scheuerlein, A., Van't Hof, T. J., & Gwinner, E. (2001). Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*). *Proceedings of the Royal Society of London B: Biological Sciences*, 268, 1575-1582. https://doi.org/10.1098/rspb.2001.1691

Segura, L. N., Di Sallo, F., Mahler, B., & Reboreda, J. (2016). Red-crested cardinals use color and width as cue to reject shiny cowbirds. *The Auk: Ornithological Advances*, 133, 308-315. https://doi.org/10.1642/AUK-15-181.1

Sih, A. (1994). Predation risk and the evolutionary ecology of reproductive behaviour. *Journal of Fish Biology*, 45, 111-130. https://doi.org/10.1111/j.1095-8649.1994.tb01087.x

Soderström, B. (1999). Artificial nest predation rates in tropical and temperate forests: a review of the effects of edge and nest site. *Ecography*, 22, 455-463. https://doi.org/10.1111/j.1600-0587.1999.tb00582.x

Soler, J. J., Møller, A. P., & Soler, M. (1999). A comparative study of host selection in the European cuckoo *Cuculus canorus*. *Oecologia*, 118, 265-276. https://doi.org/10.1007/s004420050727

Soler, M., Fernández-Morante, J., Espinosa, F., & Martín-Vivaldi, M. (2012). Pecking but Accepting the parasitic eggs may not reflect ejection failure: the role of motivation. *Ethology*, 118, 662-672. https://doi.org/10.1111/j.1439-0310.2012.02058.x

Soler, M. (2013). Long-term coevolution between avian brood parasites and their hosts. *Biological Reviews*, 89, 688-704. https://doi.org/10.1111/brv.12075

Sorenson, M. D., & Payne, R. B. (2002). Molecular genetic perspesctives on avian brood parasitism. *Integrative and Comparative Biology*, 42, 388-400. https://doi.org/10.1093/icb/42.2.388

Stevens, M. (2013). Bird brood parasitism. *Current Biology*, 23, R909-R913. https://doi.org/10.1016/j.cub.2013.08.025

Stauffer-Jr, J. R., & Loftus, W. F. (2010). Brood parasitism of a Bagrid Catfish (*Bagrus meridionalis*) by a Clariid Catfish (*Bathyclarias nyasensis*) in lake Malawi Africa. *Copeia*, 2010, 71-74. https://doi.org/10.1643//CE-09-087

Thompson III, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis*, 149, 98-109. https://doi.org/10.1111/j.1474.919X.2007.00697.x

Trivers, R. (1972). Parental investment and sexual selection. In: Campebell B (ed) Sexual Selection & the Descent of Man. Aldine Chicago, pp 136–207.

Vitousek, M. N., Jenkins, B. R., & Safran, R. J. (2014). Stress and success: individual differences in the glucocorticoid stress response predict behaviour and reproductive success under high predation risk. *Hormones and Behavior*, 66, 812-819. https://doi.org/10.1016/j.yhbeh.2014.11.004

Weller, M. W. (1959). Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. *Ecological Monographs*, 29, 333-365. https://doi.org/10.2307/1942134

Wingfield, J. C. (1984). Influence of weather on reproduction. *The Journal of Experimental Zoology*, 232, 589-594. https://doi.org/10.1002/jez.1402320327

Wingfield, J. C., Ramos-fernandez, G., & la Mora, N. A. (1999). The effects of an "El niño" Southern oscillation event on reproduction in male and female Blue-Footed Boobies, *Sula neuboxii. General and Comparative Endocrinology*, 114, 163-172. https://doi.org/10.1006/gcen.1998.7243

Yom-Tov, Y. (1980). Intraespecific nest parasitism in birds. *Biological Reviews*, 55, 93-108. https://doi.org/10.1111/j.1469-185X..1980.tb00689.x

Egg ejection cost can limit defence strategies against brood parasitism

Este manuscrito foi publicado no periódico Ethology, portanto segue as normas do mesmo.

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ABSTRACT

A cost associated with the evolution of anti-parasite strategies is the failure to recognise parasitic eggs, leading the host to evict its own eggs. However, there is evidence that birds recognize their own eggs through imprinting. This leads to the question of why birds accept parasitic eggs if such eggs can be identified. Here, we tested if egg ejection *per se* can be costly due to increased predation risk to the remaining clutch, and whether olfactory or visual cues of egg ejection increase predation. We carried out three field experiments to answer the following questions: (a) Does ejecting an egg increase nest predation risk? (b) Does the presence of olfactory cues, such as the smell of a broken egg, increase nest predation risk? and (c) Does the presence of visual cues, such as an egg shell below the nest, increase nest predation risk? We found evidence that egg ejection increases nest predation, and that olfactory cues alone also increase nest predation. The presence of visual cues did not change predation rates. These data indicate that egg ejection is costly for both host and parasitic eggs that may remain in the nest. Our results suggest why host and parasite eggs are commonly found within the same nests, despite the possibility that hosts recognize and could possibly eject the parasite’s egg.

KEY-WORDS: brood parasitism, cheating, nest predation; olfactory cues; visual cues

INTRODUCTION

A host's failure to recognize its own eggs may be the foremost obstacle involved in the evolution of defence strategies such as ejection of a parasite's eggs (Soler et al., 2014). The ability of hosts to recognise parasitic eggs is based upon estimates of ejection and/or acceptance rates of such eggs (*e.g.* Aviles & Garamszegi, 2007; Moskát et al., 2008; Spottiswoode & Stevens, 2010; Soler et al., 2012), with further refinements that involve testing the differences between the ejection rates of mimetic and non-mimetic parasite eggs (*e.g.* Vikan et al., 2009; Spottiswoode & Stevens, 2010). It remains unclear, however, whether birds accept parasitic eggs because they are unable to recognize the parasitic egg or because egg ejection is costly (Soler et al., 2012). For example, parts of the ejected egg could provide visual and olfactory cues for predators to find the nest (Weller, 1959). The process of ejection can damage the hosts' eggs (Soler et al., 2012), and once an egg is broken inside the nest, predators can use olfactory cues to find it. This scenario seems to be especially important for birds with small beaks, which may be unable to grasp and then carry the parasitic egg away from the nest or to at least drop it over the nest´s rim (Martín-Vivaldi et al., 2002).

Past studies suggest that some nest predators find nests using visual cues associated with breeding, such as the eggs (Blanco & Bertellotti, 2002; Kilner, 2006; Langen & Berg, 2016), nest morphology (Langen & Berg, 2016), and parental movements (Roper & Goldstein, 1997; Martin et al., 2000). Thus, nest predation should be primarily a daylight event. However, recent studies have shown that night predation also plays an important role in decreasing nest survival (Ribeiro-Silva et al., 2018). Given low night luminosity, nocturnal predators are more likely to use olfactory (Whelan et al., 1994; Mihailova et al., 2018), thermal (Weatherhead & Blouin-Demers, 2004; Stake et al., 2005) and auditory cues (Rice, 1982; Halupka, 1998; Briskie et al., 1999) to find nests. Defence strategies believed to be effective against olfactory tracking include reduction of parental odour (Reneerkens et al., 2005), removal of faecal sacs from the nest (Petit et al., 1989), and behavioural changes in the presence of predator odour (Godard et al., 2007; Amo et al., 2008).

Given the theoretical scope detailed above, our first objective in this study was to test if egg ejection, that is, an egg thrown out of the nest, increases predation of any eggs remaining in a nest. Second, we tested whether visual or olfactory cues associated with egg ejection by hosts could explain variation in egg predation. We carried out three field experiments to tease apart these aspects of predator nest detection based on our prediction that egg ejection would increase predation risk, and that both olfactory and visual cues would explain the increase in predation.

METHODS

Study Site

We carried out this study from October to November 2017, within the University of Brasília campus, in Brasília, Brazil (15°45'S; 47°52'W; average elevation:1020m). The vegetation in the study site is classified as Cerrado *sensu stricto* (tropical savanna) with a high diversity of woody trees (Assunção & Felfili, 2004) and presence of invasive grasses such as *Brachiaria* sp. and Molasses grass *Melinis minutiflora*. The average daily temperature is 21.5 ° C (minimum 14.0 ° C, maximum: 29.1 ° C) and average annual rainfall is 1494 mm (minimum: 1167 mm, maximum: 1801 mm) (INMET, 2017), occurring mostly during the rainy season, which in the region is from October to March. Thus, we conducted the experiment at the beginning of the rainy season, which is when the majority of birds in the Cerrado biome initiate breeding activities.

Experimental Procedure

For each of the three experiments performed (Figure 1), we used 110 artificial cotton string nests (9 cm in diameter and 3 cm in height) comprising 55 treatment and 55 control nests for each experiment. Japanese quail *Coturnix japonica* eggs were used for all experiments, as these are commercially produced and yield a large number of eggs with negligible variation in morphology. Additionally, quail eggs are similar in size to eggs of other local passerine species (Del Hoyo et al., 2018). Our treatment group included nests with egg ejection cues while the control group did not have any egg ejection cues. Each nest contained a whole, unbroken quail egg, while the cues were introduced below the nests, and included: Experiment 1: complete broken egg (eggshell + contents = visual and olfactory cues); Experiment 2: liquid component of an egg (egg contents only = olfactory cue); Experiment 3: thoroughly washed eggshell halves (eggshell only = visual cue). We assume that despite the fact that egg contents (experiment 2) were visible immediately after setting up the experiment, they would provide a negligible visual cue, since exposure to the high field temperature (typical of the Cerrado biome) would dry out the liquid contents over a few hours, leaving only olfactory cues. The eggshell washing (experiment 3) consisted of three procedures: the eggshells were first washed with water only, followed by cleaning with water and a neutral detergent (diluted at 10:1), and finally a water wash to remove any remaining odours. The eggshell was then dried overnight at room temperature.

Each experiment was conducted on a different day, between 0800 and 1500 hours, and the artificial nests were attached to shrub branches at heights of approximately 40 cm (range: 15 – 65 cm), a common nest height for small passerines in the region. The experimental nests, once set up, remained in the field for 72 hours after which we collected the data. Given the possibility of natural variations in weather condition that could affect predator performance to reach the nest, we only compared data from the treatment and control trials within the same experiment, that is, conducted simultaneously.

We assumed that predation occurred when the egg disappeared from the nest. Predation was not assumed when only the egg ejection cue disappeared (n = 2 in experiment 3), but an egg remained in the nest. We organized the nest points by interspersing control and experimental nests. To avoid predators learning the location of nests along the transects, we placed them 50 m apart, and the transects were moved approximately 23 m for each consecutive experiment.

Statistical Analyses

For each experiment, we examined the differences in predation levels between treatment and control groups using a chi-square test, conducted in R software version 3.5.0 (R Core Team, 2018). The alpha level was set at p = 0.05.

RESULTS

We detected a significant increase in predation of intact eggs inside the nest when a whole egg was broken beneath the nest (p = 0.042), and when only egg contents were on the ground (p = 0.006). No significant differences were detected between control nests and those in the treatment that had the washed eggshell under the nest (p =

0.095) See table 1. Thus, our evidence indicates that the presence of complete broken eggs (experiment 1), as well as egg contents (experiment 2) modify predation rates of unbroken eggs within a nest. The presence of only washed eggshells (i.e., just the visual cue) did not influence predation rates of the nests (experiment 3).

DISCUSSION

In this study we found clear evidence that, even in the absence of parents at the nest, egg ejection increases predation risk for other eggs that remain. Our results suggest that egg ejection is costly for any remaining eggs in the nest, regardless of whether they are from hosts or brood parasites. These results may explain why, in at least some circumstances, hosts may not eject parasitic eggs even when they may potentially have the ability to identify them.

Tests of self-egg recognition indicate that some host species are able to recognize parasitic eggs (Aviles & Garamszegi, 2007) based upon differences in egg size, eggshell spot pattern (de la Colina et al., 2012; De Mársico et al., 2016) or odour (Soler et al., 2014). Some host species accept the parasitic egg but then do not provide parental care. For instance, females of American coots *Fulica americana* push parasitic eggs to poorer incubation positions at the outer edge of the clutch (Lyon, 2003). Eastern bluebirds *Sialia sialis* also do not eject parasitic eggs, but move them to peripheral areas of the nest box where they are not incubated (Siefferman, 2006). Additional strategies involve neglecting the parasitic offspring, as found in a study of the great reed warbler, *Acrocephalus arundinaceus*, where parents delivered less food for parasite chicks than would be expected in random food distribution between offspring (Hauber & Moskát, 2007).

Contrary to one of our predictions, we found that the increase in predation occurred only when a whole egg was ejected or due specifically to olfactory cues, and that the visual cue was not important. This differs from a few studies that associate predation with visual components of nests and/or eggs (De Mársico et al., 2016; Langen & Berg, 2016). There are three possible explanations for this divergence. First, our experimental setup lacked elements typically associated with natural nests, such as movement, sounds, and parental odours. Secondly, we introduced visual cues outside the nests, while many studies have evaluated visual components associated directly to the nest (Honza et al., 2011). Finally, it’s also possible that on our field site, the majority of predators are nocturnal, and nest tracking is primarily based on olfactory cues (Whelan et al., 1994).

In conclusion, our results suggest that egg ejection entails fitness costs for both hosts and parasites. Increased clutch predation after egg ejection presents a dilemma for the host, where they have to choose between accepting the additional cost represented by keeping the parasitic egg in the current breeding attempt or abandoning the entire clutch to initiate a new breeding attempt. Natural predation rates differ between habitats, and in our study site, typical predation rates may exceed 70% of nests (Lopes & Marini, 2005; Macedo et al., 2012; Diniz et al., 2013). Future studies should explore whether egg ejection also increases predation in areas with low predation rates. In this study we did not identify predators that could be favoured by each type of egg ejection cue, and the use of trap cameras could be useful in this regard.

REFERENCES

Amo, L., Galván I., Tomás G. & Sanz J. (2008). Predator odour recognition and avoidance in a songbird. *Functional Ecology*, 22, 289-293. https://doi.org/10.1111/j.1365-2435.2007.01361.x

Assunção, S. L., & Felfili, J. M. (2004). Fitossociologia de um fragmento de cerrado sensu stricto na APA do Paranoá, DF, Brasil. *Acta Botanica Brasilica*, 18, 903-909. http://dx.doi.org/10.1590/S0102-33062004000400021.

Aviles, J. M., & Garamszegi, L. Z. (2007). Egg rejection and brain size among potential hosts of the common cuckoo. *Ethology*, 113, 562-572. https://doi.org/10.1111/j.1439-0310.2007.01359.x

Blanco, G., & Bertellotti, M. (2002). Differential predation by mammals and birds: implications for egg-colour polymorphism in a nomadic breeding seabird. *Biological Journal of the Linnean Society*, 75, 137-146. https://doi.org/10.1046/j.1095-8312.2002.00026.x

Briskie, J. V., Martin, P.R., & Martin, T. E. (1999). Nest predation and the evolution of nestling begging calls. *Proceedings of the Royal Society of London B: Biological Sciences*, 266, 2153-2159. https://doi.org/10.1098/rspb.1999.0902

de la Colina, M.A., Pompilio, L., Hauber, M.E., Reboreda, J. C., & Mahler, B. (2012). Different recognition cues reveal the decision rules used for egg rejection by hosts of a variably mimetic avian brood parasite. *Animal Cognition*, 15, 881-889. https://doi.org/10.1007/s10071-012-0515-9.

De Mársico, M. C., Ursino, C. A., & Reboreda, J. C. (2016). Experimental evidence for an antipredatory function of egg rejection behaviour in a common host of the brood-parasitic shiny cowbird. *Behav Ecol Sociobiol*, 70, 1689-1697. https://doi.org/10.1007/s00265-016-2174-3.

Del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & de Juana, E. (2018). Handbook of the Birds of the World Alive. In. Lynx Edicions, Barcelona.

Diniz, P., Ramos, D. M., & Chemin, N. (2013). Breeding biology of Coal-crested Finches. *The Wilson Journal of Ornithology*, 125, 592-599.

Godard, R. D., Bowers, B. B., & Morgan, W. C. (2007). Eastern bluebirds Sialia sialis do not avoid nest boxes with chemical cues from two common nest predators. *Journal of Avian Biology*, 38, 128-131. https://doi.org/10.1111/j.2007.0908-8857.03788.x

Halupka, K. (1998). Vocal begging by nestlings and vulnerability to nest predation in Meadow Pipits Anthus pratensis; to what extent do predation costs of begging exist? *Ibis*, 140, 144-149. https://doi.org/10.1111/j.1474-919X.1998.tb04552.x

Hauber, M. E., & Moskát, C. (2007). Shared parental care is costly for nestlings of common cuckoos and their great reed warbler hosts. *Behavioral Ecology*, 19, 79-86. https://doi.org/10.1093/beheco/arm108

Honza, M., Procházka, P., Morongová, K., Čapek, M., & Jelínek, V. (2011). Do nest light conditions affect rejection of parasitic eggs? a test of the light environment hypothesis. *Ethology*, 117, 539-546. https://doi.org/10.1111/j.1439-0310.2011.01900.x

INMET INdM (2017) Banco de Dados Meteorológicos para Ensino e Pesquisa, Data from 2000-2016. In, Brasília.

Kilner, R. M. (2006). The evolution of egg colour and patterning in birds. *Biological Reviews*, 81, 383-406. https://doiorg/101017/S1464793106007044

Langen, T. A., & Berg, E. C. (2016). What determines the timing and duration of the nesting season for a tropical dry forest bird, the White-throated Magpie-Jay (*Calocitta formosa*)? *The Wilson Journal of Ornithology*, 128, 32-42. https://doi.org/10.1676/wils-128-01-32-42.1

Lopes, L. E., & Marini, M. A. (2005) Low reproductive success of Campo Suiriri (*Suiriri affinis*) and Chapada Flycatcher (*S. islerorum)* in the central Brazilian Cerrado. *Bird Conservation International*, 15, 337-346. https://doi.org/10.1017/S0959270905000675

Lyon, B. E. (2003). Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature*, 422, 495-499. https://doi.org/10.1038/nature01505

Macedo, R. H., Manica, L., & Dias, R. I. (2012). Conspicuous sexual signals in a socially monogamous passerine: The case of neotropical Blue-black Grassquits. *Journal of Ornithology*, 153, 15-22. https://doi.org/10.1007/s10336-012-0815-5

Martín-Vivaldi, M., Soler, M., & Møller, A. P. (2002). Unrealistically high costs of rejecting artificial model eggs in cuckoo *Cuculus canorus* hosts. *Journal of Avian Biology*, 33, 295-301. https://doi.org/10.1034/j.1600-048X.2002.330311.x

Martin, T. E., Martin, P., Olson, C., Heidinger, B., & Fontaine, J. (2000). Parental care and clutch sizes in North and South American birds. *Science*, 287, 1482-1485.

Mihailova, M., Berg, M. L., Buchanan, K. L., & Bennett, A. T. (2018). Olfactory eavesdropping: The odor of feathers is detectable to mammalian predators and competitors. *Ethology*, 124, 14-24. https://doi.org/10.1111/eth.12701

Moskát, C., Hansson, B., Barabás, L., Bártol, I., & Karcza, Z. (2008). Common cuckoo *Cuculus canorus* parasitism, antiparasite defence and gene flow in closely located populations of great reed warblers *Acrocephalus arundinaceus*. *Journal of Avian Biology*, 39, 663-671. https://doi.org/10.1111/j.1600-048X.2008.04359.x

Petit, K. E., Petit, L. J., & Petit, D. R. (1989). Fecal Sac Removal: Do the Pattern and Distance of Dispersal Affect the Chance of Nest Predation? *The Condor*, 91, 479-482. https://doi.org/10.2307/1368991

R Core Team (2018). R: a language and environment for statistical computing. R foundation for statical computing, Viena, Austria.

Reneerkens, J., Piersma, T., & Damsté, J. S. S. (2005). Switch to diester preen waxes may reduce avian nest predation by mammalian predators using olfactory cues. *Journal of Experimental Biology*, 208, 4199-4202. https://doi.org/10.1242/jeb.01872

Ribeiro-Silva, L., Perrella, DF., Biagolini-Jr, C. H., Zima, P. V. Q., Piratelli, A. J., Schlindwein, M. N., Galetti, J. P. M., & Francisco, M. R. (2018). Testing camera traps as a potential tool for detecting nest predation of birds in a tropical rainforest environment. *Zoologia*, 35, 1-8. https://doi.org/10.3897/zoologia.35.e14678

Rice, W. R. (1982). Acoustical location of prey by the marsh hawk: adaptation to concealed prey. *The Auk*, 403-413.

Roper, J. J., & Goldstein, R. R. (1997). A test of the Skutch hypothesis: does activity at nests increase nest predation risk? *Journal of Avian biology*, 111-116. https://doi.org/10.2307/3677304

Siefferman, L. (2006). Egg coloration and recognition of conspecific brood parasitism in eastern bluebirds. *Ethology*, 112, 833-838. https://doi.org/10.1111/j.1439-0310.2006.01229.x

Soler, J., Pérez, C. T., De Neve, L., Macías, S. E., Møller, A., & Soler, M. (2014). Recognizing odd smells and ejection of brood parasitic eggs. An experimental test in magpies of a novel defensive trait against brood parasitism. *Journal of Evolutionary Biology*, 27, 1265-1270. https://doi.org/10.1111/jeb.12377

Soler, M., Fernández-Morante, J., Espinosa, F., & Martín-Vivaldi, M. (2012). Pecking but Accepting the Parasitic Eggs may not Reflect Ejection Failure: The Role of Motivation. *Ethology*, 118, 662-672. https://doi.org/10.1111/j.1439-0310.2012.02058.x

Spottiswoode, C. N., & Stevens, M. (2010). Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 8672-8676. https://doi.org/10.1073/pnas.0910486107

Stake, M. M., Thompson, F. R., Faaborg, J., & Burhans, D. E. (2005). Patterns of snake predation at songbird nests in Missouri and Texas. *Journal of Herpetology*, 39, 215-222. https://doi.org/10.1670/150-04A

Vikan, J. R., Stokke, B. G., Fossøy, F., Jackson, C., Huhta, E., Rutila, J., Moksnes, A., & Røskaft, E. (2009). Fixed rejection responses to single and multiple experimental parasitism in two fringilla hosts of the common cuckoo. *Ethology*, 115, 840-850. https://doi.org/10.1111/j.1439-0310.2009.01679.x

Weatherhead, P. J., & Blouin-Demers, G. (2004). Understanding avian nest predation: why ornithologists should study snakes. *Journal of Avian Biology*, 35, 185-190. https://doi.org/10.1111/j.0908-8857.2004.03336.x

Weller, M. W. (1959). Parasitic egg laying in the Redhead (*Aythya americana*) and other North American Anatidae. *Ecological Monographs*, 29, 333-365. https://doi.org/10.2307/1942134

Whelan, C. J., Dilge, M. L., Robson, D., Hallyn, M. N., & Dilge, S. (1994). Effects of Olfactory Cues on Artificial-Nest Experiments. *The Auk*, 945-952.

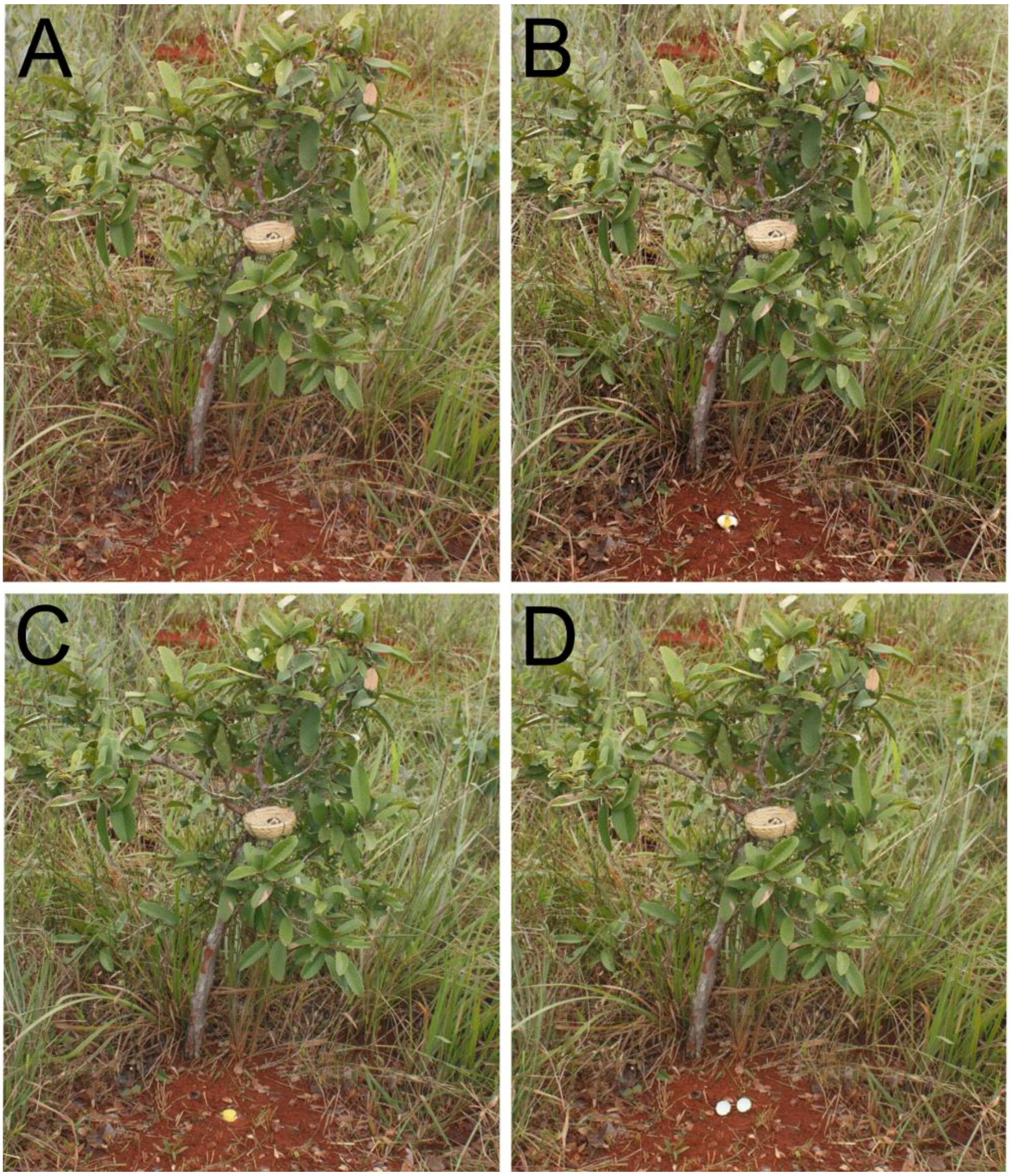
Table 1. Observed predation rates (% of depredated nests) and chi-square results for comparison of predation levels between treatment and control groups in three experiments-all experiments had 55 treatment and 55 control nests.

	Experiment 1		Experiment 2		Experiment 3	
	Predation level	Chi-square test	Predation level	Chi-square test	Predation level	Chi-square test
Treatment	20.00	$X^2 = 4.15$	34.55	$X^2 = 7.45$	12.73	$X^2 = 2.78$
Control	5.36	$p = 0.042$	10.91	$p = 0.006$	27.27	$p = 0.095$

Note. In each experiment, all nests contained one whole quail egg, while the cues were introduced below the nests of treatment groups and included Experiment 1: complete broken egg; Experiment 2: Liquid content of the egg; and Experiment 3: Thoroughly washed eggshell halves.

Figure legend

Figure 1. Representation of difference between control and treatment for each experiment. (a) Control for all experiments: artificial nest of 9 cm in diameter and 3 cm in height, placed in shrubs, without egg ejection cue. (b) Experiment 1: introduction of a complete broken egg under artificial nest (eggshell+ contents = visual and olfactory cues). (c) Experiment 2: introduction of a liquid component of an egg (egg contents only = olfactory cue). (d) Experiment 3: introduction of a washed eggshell under artificial nest (eggshell only = visual cue)



Parental presence and conspicuous coloration do not increase nest predation risk

Esse manuscrito foi submetido ao periódico Ethology, portanto segue as normas do mesmo.

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ABSTRACT

To improve reproductive success and maximize offspring survivorship, bird parents have to deal with the threat of nest predation while caring for nestlings, which necessarily involves their presence near the nest. On the other hand, predators may use cues such as parental movement near the nest and conspicuous coloration of individuals to find nests. Although conspicuous coloration in males may confer advantages in male-male competition or mate choice, it may also have survival costs for the males or their offspring, especially when predators are visually oriented. In this study, we carried out a field experiment to test the possibility that visual cues attract predators to nests and impose a higher risk to eggs and offspring. By using painted styrofoam balls as a proxy for parents and artificial nests baited with quail eggs, we addressed the following conceptual questions: (1) Does the presence of parents in the nest increase the risk of nest predation? (2) Does the presence of conspicuously-colored parents in the nest increase the risk of nest predation? Based on our experimental results, we rejected the hypotheses that parents and conspicuous coloration increase nest predation rates. The presence of "parents" in the nest and conspicuousness (bright red color) did not impose additional risks to eggs in the nest. We suggest that predators in the area may be olfactory oriented, and that absence of parental movements and other possible cues may explain our results.

Key Words: Birds, Bright colors, Camouflage colors, Predation, Reproductive success, Visual cues.

INTRODUCTION

Nest predation is one of the major selective forces that results in reproductive failure for birds (Ricklefs, 1969; Martin, 1993; Thompson III, 2007). To find nests efficiently, predators use their sensory mechanisms to detect a variety of cues, which may be visual (Czapliki & Porter, 1974; Mullin & Cooper, 1998), olfactory (Rangen et al., 2000; Hamilton et al., 2002), thermal (Weatherhead & Blouin-Demers, 2004; Stake et al., 2005) and auditory (Leech & Leonard, 1997; Husby, 2018). While predatory mammals rely mainly on visual and olfactory cues (Whelan et al., 1994), predatory birds usually use auditory and visual cues, which in the latter case includes the observation of parental activity in the vicinity of nests (Martin et al., 2000; Santisteban et al., 2002).

A key factor that should be taken into account when considering male birds conducting parental activities is that they often exhibit secondary sexual characteristics (*e.g.* vibrant colors and/or ornaments) that may possibly attract predators. Such attributes may be maintained in a population both by intra and intersexual selection (Keyser & Hill, 2000) and may represent honest signs of quality of a male in a mating context (Møller & Nielsen, 1997; Magalhães et al., 2014). Studies show that more conspicuous individuals are able to produce larger broods (Broggi & Senar, 2009), exhibit higher rates of parental care (Sundberg & Larsson, 1994; Pagani-Núñez & Senar, 2016), defend territories of better quality and with higher prey abundance (Keyser & Hill, 2000), have higher social dominance (Kraaijeveld et al., 2004; Stuart-Fox & Moussalli, 2008) and obtain more extra-pair copulations (Weatherhead & Boag, 1995; Yezerinac & Weatherhead, 1997). These studies indicate that being a conspicuous male may confer reproductive advantages in comparison with more cryptic individuals.

However, when considering predation risk, there is a conflict between the attractive conspicuous plumage due to sexual selection and the cryptic plumage that could be produced via natural selection (Zahavi, 1975; Andersson, 1994). Although attractive male features may favor successful mating and confer higher reproductive success, a conspicuous individual is also potentially easier to be detected by predators that use visual cues during hunting. Thus, there is an expected trade-off between the intensity of coloration of an individual and predation risk to the parents and their nestlings (Yasukawa, 2017).

The "selection trade-off hypothesis" suggests that males will be more ornamented in habitats with lower predation risk and that females will select such traits; however, in habitats with high predation risk the opposite will occur (Heinen-Kay et al., 2015). Several studies have substantiated this hypothesis, suggesting that differences in coloration among several taxonomic groups reflect an adjustment between the level of coloration and the risk of predation by visual predators (Endler, 1987; Hansson, 2000; Stuart-fox & Ord, 2004). A few studies, however, have not supported this idea. For example, studies with the azure-winged magpie (*Cyanopica cyanus*) and the American yellow warbler (*Setophaga petechia*), both intensely colored species, show that in some cases more conspicuous individuals did not reduce their rate of parental activity even in high predation risk contexts (Avilés et al., 2008, Grunst et al., 2015).

Although nest predation rates have typically been assumed to be higher for tropical birds when compared to birds in temperate regions (Ricklefs, 1969; Skutch, 1985; Martin, 1995), our current knowledge of nest predation rates in the tropics is actually very scarce. Higher nest predation in tropical birds is presumed to occur as a result of the more diverse predator fauna found in tropical habitats (Skutch, 1949; Snow & Snow, 1964; Ricklefs, 1969). This perceived contrast in nest predation rates in tropical versus temperate regions has been used to support numerous hypotheses about life history strategies of tropical birds, such as smaller clutch sizes and repeated nesting attempts (Söderström, 1999). Here, we address one of the gaps in knowledge relative to nest predation in tropical birds, which concerns how potential predators might find nests. A recent experimental study in the central savanna (Cerrado) biome of Brazil showed that olfactory cues, in the form of broken eggs, increased nest predation rates (Biagolini-Jr & dos Santos, 2018). The study, however, found no relation between nest predation rates when visual cues, in the form of eggshells, were introduced below the nests. However, the question of whether visual cues more specifically indicative of parents near the nest would be associated with higher predation risk remained unanswered.

To address this question, we performed a field experiment to assess the effect of visual cues more directly associated with nests on rates of nest predation. The cues we used were physically connected to the nests, simulating the presence of either conspicuous (brightly colored) or cryptic (dull colored) parents at the nests in contrast to the absence of parents. Considering the details above and costs and benefits of exhibiting conspicuous coloration, the objectives of our study were to: (1) identify differences in nest predation rates in the presence or absence of parents; and (2) detect if different colorations of parents could influence nest predation rates. We hypothesized that (i) nest predation rates are higher when parents are at the nest and (ii) when they present a conspicuous coloration, in contrast with rates for nests where parents are absent or cryptic.

METHODS

Study site

This study was carried out in November 2018, in the Campus of the University of Brasilia (UnB), in Brasília, Brazil (15°45'S; 47°52'W; average altitude of 1020 m: minimum = 959, maximum = 1081). Nests in this area are subject to high rates of predation that range from approximately 54% to 80% (Lopes & Marini, 2005; Macedo et al., 2012; Diniz et al., 2013). The total sum of the selected areas for this experiment is of approximately 32 ha. The predominant habitat is a shrubby savanna vegetation known as Cerrado *sensu stricto*, which includes a wide range of species of woody trees (Assunção & Felfili, 2004) and invasive grasses, such as *Brachiaria* sp. and *Melinis minutiflora*. Thermal amplitude is between 14.0ºC and 29.1ºC (average daily: 21.5°C) and annual average rainfall is approximately 1494 mm (minimum: 1167 mm, maximum: 1801 mm) (INMET, 2017).

Experimental procedure

We selected previously georeferenced points at the study area to install artificial nests. These points were 50 m apart to maximize the independence of sampling units. The experiment was repeated three times in order to increase the reliability of the results. To avoid habituation of predators to the nests and to maximize the use of the area, we displaced the points by 23.5 m in each campaign.

For each campaign we installed three groups of cotton string artificial nests (9 cm in diameter and 3 cm in height): (1) control group, with no visual cues; (2) cryptic coloration treatment group; and (3) conspicuous coloration treatment group. In each campaign, number of nests placed for each group were (N_1 = 20, N_2 = 26, N_3 = 36) totalizing 82 nests per group and 246 nests in total (Figure 1). The visual cues fixed above the nests and representing the parents were either bright red (conspicuous) or dark brown (cryptic) styrofoam balls. These were painted with acrylic paint and sealed with varnish 72 hours before the experiment was conducted. To avoid loss of coloration before each campaign we checked the balls for possible damages and retouched the paint to ensure the exact coloration between campaigns.

We installed nests between 0800 and 1700 h of each day on shrubs at an average height of ~ 40 cm (range: 15-65 cm), height at which small passerines in this region build their nests, and placed two quail (*Coturnix japanica*) eggs in each nest. The nests were exposed in the field for 72 hours after which they were checked to verify whether predation had occurred. We used quail eggs because they are easy to acquire and because of their resemblance in size to small Passeriformes eggs present in the study area (e.g. *Mimus sp.* and *Turdus sp*.). We considered a predation event when at least one of the eggs disappeared from the nest or when eggshells were found nearby (methodology adapted from Biagolini-Jr & dos Santos, 2018).

Statistical analyses

To verify statistical differences in rates of nest predation between control and treatment groups, we utilized a chi-square test with Yates' continuity correction. Tests were conducted in R software version 3.5.0 (R Core Team, 2018). The alpha level used was set at $p = 0.05$.

RESULTS

We did not find significant differences in nest predation rates between control and treatment groups when "parents" were present at the nest ($p = 0.944$) (Table 1; hypothesis 1). Additionally, no significant differences were found when "parents" exhibited conspicuous versus cryptic colorations ($p = 0.474$) (Table 1; hypothesis 2).

DISCUSSION

Our results indicate that the presence and conspicuous coloration of cues representing parents do not increase nest predation rates. The questions raised in this study resulted from a previous finding reported in a nest predation experiment conducted in the same area (Biagolini-Jr & dos Santos, 2018), which concluded that visual cues below the nest, in the form of broken eggshells, did not attract predators. Our experiment further confirms this idea, since conspicuous visual cues now placed right above the nest produced similar results.

One plausible explanation for this finding is that the predators in the area where the experiment was conducted may not be visually oriented; in other words, they use other sensory mechanisms involving auditory or olfactory cues to find their prey (e.g. nocturnal mammals) (Reneerkens et al., 2005). Another possibility is that the movement of parents can be of critical importance for predators to locate nests, and our cues were static.

Nest-associated odors, including that of the adult birds or nestlings, ejected and broken eggs on the ground and fecal sacs were absent in our experiment. Such odors may increase the chances of nest predation (Reneerkens et al., 2005; Ibáñez-Álamo et al., 2013; Biagolini-Jr & dos Santos, 2018). Our experiment also did not include the presence of offspring and their corresponding activities, which include begging calls. Offspring and parental acoustic activity can attract auditory predators to the nest and impose higher predation risks (Leech & Leonard, 1997; Husby, 2018). Parental movements, such as foraging and feeding of nestlings, were also absent in our study. Parents may reduce their activities near the nest when predation risk is higher (Eggers et al., 2005; Grunst et al., 2015; Ibáñez-Álamo & Soler, 2017), and the absence of parental activities makes it more difficult for predators to find the nests (Colombelli-Negrel & Kleindorfer, 2009). Others traits related to parental activity and nests that could not be tested here but that can attract more predators to the nest are nest building activity, nest size, clutch size, and length of incubation and hatchling periods (Cresswell, 1997).

The lack of difference in nest predation rates between nests associated with conspicuous versus cryptic “parents” was more puzzling. In the absence of olfactory cues, we expected that visual predators would be more actively targeting the nests containing the bright red cues. The Batesian mimicry hypothesis (Bates, 1981) may provide a possible explanation for this result. According to this hypothesis, predators may avoid prey (that are frequently edible) that exhibit aposematic coloration, as this could indicate a noxious species (Lindström et al., 1999). Furthermore, predators may also prefer familiar prey, avoiding unknown species (Stuart-fox et al., 2003). Habituation to new and rare prey requires time (Götmark & Olson, 1997).

Our study thus suggests that the relationship between conspicuousness and predation is not a straightforward one. While some studies have found a positive relationship between conspicuousness and predation rate, other studies have found opposite relationships (Götmark 1993, 1994; Huhta et al., 2003; Slagsvold et al., 2005). In some cases, coloration based on carotenoids and melanin, which are responsible for bright colors, are related to traits such as boldness, which result in conspicuous parents being exposed to higher predation risks, but which also exhibit elevated rates of parental care, higher ability in avoiding predators and a propensity to engage in agonistic behaviors and attack predators (Fowler-Finn & Hebets, 2011; Mafli et al., 2011; Da silva et al., 2013; Pagani-Núñez & Senar, 2016; Mcqueen et al., 2017).

A high degree of synergy also appears to occur between multiple variables and nest predation. Nest site may influence nest predation events, and both of these may determine parental activities. In the American yellow warbler (*Setophaga petechia*), for instance, more conspicuous individuals reduce their parental activities when nests are built on the ground since it appears they are more exposed to predators than when nests are built in trees (Haskell, 1996; Grunst et al., 2015). Background and shading color of the environment is another factor that may limit the perception of vibrant coloration. In places where the environmental background is complex and includes a more diverse color spectrum, males may exhibit more conspicuous colors without suffering higher predation rates (Husak et al., 2006).

In conclusion, despite the numerous studies that suggest that conspicuousness and parental activities lead to higher predation rates in nests, our experiment did not support the notion that conspicuousness, in itself, increases the chances of predators finding nests. Considering the tropical savanna area where we conducted our experiment, we thus suggest that male conspicuousness could be advantageous in the context of mate selection, since coloration appears to be irrelevant as a cue to local predators, possibly because of their sensory mechanisms. Nest predators in the Neotropics include over 200 species of birds, reptiles, mammals and arthropods (Menezes and Marini, 2017). However, a more refined identification of local nest predators would be helpful to determine which category of sensorial cues could most likely lead to nest predation. Future studies should consider the use of camera traps to identify the most abundant predators in specific tropical habitats. Additionally, it would be useful to compare different kinds of eggs that emit specific olfactory cues (e.g. plasticine and quail eggs). In addition, other kinds of stimuli, such as the presence of offspring, parental vocal activity and movement near the nest may be important cues that should be taken into consideration and further examined.

REFERENCES

Andersson, M. (1994). Sexual selection. Princeton University Press, Princenton, NJ.

Avilés, J. M., Solís, E., Valencia, J., de la Cruz, C., & Sorci, G. (2008). Female and male plumage brightness correlate with nesting failure in azure-winged magpies *Cyanopica cyanus. Journal of Avian Biology*, 39, 257-261. https://doi.org/10.1111/j.0908-8857.2008.04218.x

Assunção, S. L., & Felfili, J. M. (2004). Fitossociologia de um fragmento de cerrado sensu stricto na APA do Paranoá, DF, Brasil. *Acta Botanica Brasilica*, 18, 903-909. https://dx.doi.org/10.1590/S0102-33062004000400021

Bates, H. W. (1981). Contributions to an insect fauna of the amazon valley (Lepidoptera: Heliconidae). *Biological Journal of the Linnean Society*, 16, 41-54. https://doi.org/10.1111/j.1095-8312.1981.tb01842.x

Biagolini-Jr, C., & dos Santos, P. V. R. (2018). Egg ejection cost can limit defence strategies against brood parasitism. *Ethology*, 124, 719-723. https://doi.org/10.1111/eth.12803

Broggi, J., & Senar, J. C. (2009). Brighter great tits parents build bigger nests. *Ibis*, 151, 588-591. https://doi.org/10.1111/j.1474-919X.2009.00946.x

Cresswell, W. (1997). Nest predation rates and nest detectability in different stages of breeding in blackbirds *Turdus merula*. *Journal of Avian Biology*, 28, 296-302. https://doi.org/10.2307/3676942

Colombelli-Negrel, D., & Kleindorfer, S. (2009). Nest height, nest concealment, and predator type predict nest predation in superb fairy-wrens (*Malurus cyaneus*). *Ecological Research*, 24, 921-928. https://doi.org/10.1007/s11284-008-0569-y

Czapliki, J. A., & Porter, R. H. (1974). Visual cues mediating the selection of goldfish (*Carassius auratus*) by two species of *Natrix*. *Journal of Herpetology*, 8, 129-134. https://doi.org/10.2307/1562808

Da silva, A., Van den brink, V., Emaresi, G., Luzio, E., Bize, P., Dreiss, A. N., & Roulin, A. (2013). Melanin-based colour polymorphism signals aggressive personality in nest and territory defence in the tawny owl (*Strix aluco*). *Behavioral Ecology and Sociobiology*, 67, 1041-1052. https://doi.org/10.1007/s00265-013-1529-2

De Társico, M. C., Ursino, C. A., & Reboreda, J. C. (2016). Experimental evidence for an antipredatory function of egg rejection behaviour in a common host of the brood-parasitic shiny cowbird. *Behavioral Ecology and Sociobiology*, 70, 1689-1697. https://doi.org/10.1007/s00265-016-2174-3

Diniz, P., Ramos, D. M., & Chemin, N. (2013). Breeding biology of coal-crested finches. *The Wilson Journal of Ornithology*, 125, 592-599. https://doi.org/10.1676/12-166.1

Donald, P. F., Evans, A. D., Muirhead, L. B., Buckingham, D. L., Kirby, W. B, & Schmitt, S. I. A. (2002). Survival rates, causes of failure and productivity of skylark *Alauda arvensis* nests on lowland farmland. *Ibis*, 144, 652-664. https://doi.org/10.1046/j.1474-919X.2002.00101.x

Eggers, S., Griesser, M., Andersson, T., & Ekman, J. B. (2005). Nest predation and habitat change interact to influence Siberian jay numbers. *Oikos*, 111, 150-158. https://doi.org/10.1111/j.0030-1299.2005.13802.x

Endler, J. A. (1987). Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). *Animal Behaviour*, 35, 1376-1385. https://doi.org/10.1016/S0003-3472(87)80010-6

Fowler-Finn, K. D., Hebets, E. A. (2011). More ornamented males exhibit increased predation risk and antipredatory escapes, but not greater mortality. *Ethology*, 117, 102-114. https://doi.org/10.1111/j.1439-0310.2010.01852.x

Götmark, F. (1993). Conspicuous coloration in male birds is favoured by predation in some species and disfavoured in others. *Proceedings of the Royal Society B: Biological Sciences*, 253, 143-146. https://doi.org/10.1098/rspb.1993.0094

Götmark, F. (1994). Does a novel bright colour patch increase or decrease predation? Red wings reduce predation risk in European blackbirds. *Proceedings of the Royal Society B: Biological Sciences*, 256, 83-87. https://doi.org/10.1098/rspb.1994.0053

Götmark, F., & Olson, J. (1997). Artificial colour mutation: do red-painted great tits experience increased or decreased predation risk. *Animal Behaviour*, 53, 83-91. https://doi.org/10.1006/anbe.1996.0280

Grunst, A. S., Grunst, M. L., & Rotenberry, J. T. (2015). Sexual pigmentation and parental risk-taking in yellow warblers *Setophaga petechia*. *Journal of Avian Biology*, 46, 9-17. https://doi.org/10.1111/jav.00496

Hamilton, A. M., Freedman, A. H., & Franz, R. (2002). Effects of deer feeders, habitat and sensory cues on predation rates on artificial turtle nests. *The American Midland Naturalist,* 147, 123-134. https://doi.org/10.1674/0003-0031(2002)147[0123:EODFHA]2.0.CO;2

Hansson, L. A. (2000). Induced pigmentation in zooplankton: a trade-off between threats from predation and ultraviolet radiation. *Proceedings of the Royal Society of London B: Biological Sciences*, 267, 2327-2331. https://doi.org/10.1098/rspb.2000.1287

Haskell, D. G. (1996). Do bright colors at nests incur a cost due to predation?. *Evolutionary Ecology*, 10, 285-288. https://doi.org/10.1007/BF01237685

Heinen-Kay, J. L., Morris, K. E., Ryan N. A., Byerley, S. L., Venezia, R. E, Peterson, M. N., & Langerhans, R. B. (2015). A trade-off between natural and sexual selection underlies diversification of a sexual signal. *Behavioral Ecology*, 26, 533-542. https://doi.org/10.1093/beheco/aru228

Huhta, E., Rytkönen, S., & Solonen, T. (2003). Plumage brightness of prey increases predation risk: an among-species comparison. *Ecology*, 84, 1793-1799. https://doi.org/10.1890/0012-9658(2003)084[1793:PBOPIP]2.0.CO;2

Husak, F. J., Macedonia, J. M., Fox, S. F., & Sauceda, R. C. (2006). Predation costs of conspicuous male coloration in collared lizards (*Crotaphytus collaris*): an experimental test using clay-covered model lizards. *Ethology*, 112, 572-580. https://doi.org/10.1111/j.1439-0310.2005.01189.x

Husby, M. (2018). Nestling begging calls increase predation risk by corvids. *Animal Biology*, 68, 1-19. https://doi.org/10.1163/15707563-20181058

Ibáñez-Álamo, J. D., Sanllorente, O., Arco, L. & Soler, M. (2013). Does nest predation risk induce parent birds to eat nestlings' fecal sacs? An experimental study. *Annales Zoologici Fennici*, 50, 71-78. https://doi.org/10.5735/086.050.0106

Ibáñez-Álamo, J. & Soler, M. (2017). Male and female blackbirds (*Turdus merula*) respond similarly to the risk of nest predation. *Journal of Ornithology*, 158, 533-539. https://doi.org/10.1007/s10336-016-1403-x

Inmet INdM (2017) Banco de Dados Meteorológicos para Ensino e Pesquisa, Data from 2000-2016. Brasília.

Keyser, A. J., & Hill, G. E. (2000). Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology*, 11, 202-209. https://doi.org/10.1093//beheco/11.2.202

Kraaijeveld, K., Gregurke, J., Hall, C., Komdeur, J., & Mulder, R. A. (2004). Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behavioral Ecology*, 15, 380-389. https://doi.org/10.1093/beheco/arh023

Leech, S. M., & Leonard, M. L. (1997). Begging and the risk of predation in nestling birds. *Behavioral Ecology*, 8, 644-646. https://doi.org/10.1093/beheco/8.6.644

Lindström, L., Alatalo, R. V., & Mappes, J. (1999). Reactions of hand-reared and wild-caught predators toward warningly colored, gregarious, and conspicuous prey. *Behavioral Ecology*, 10, 317-322. https://doi.org/10.1093/beheco/10.3.317

Lopes, L. E., & Marini, M. A. (2005). Biologia reprodutiva de *Suiriri affinis* e *S. islerorum* (Aves: Tyrannidae) no cerrado do Brasil central. *Papéis Avulsos de Zoologia (São Paulo)*, 45, 127-141. http://dx.doi.org/10.1590/S0031-10492005001200001

Macedo, R. H., Manica, L. T., & Dias, R. I. (2012). Conspicuous sexual signals in a socially monogamous passerine: the case of neotropical blue-black grassquits. *Journal of Ornithology*, 153, 15-22. https://doi.org/10.1007/s10336-012-0815-5

Mafli, A., Wakamatsu K., & Roulin, A. (2011). Melanin-based coloration predicts aggressiveness and boldness in captive eastern Hermann's tortoises. *Animal Behaviour*, 81, 859-863. https://doi.org/10.1016/j.anbehav.2011.01.025

Magalhães, R. B., Diniz, P., & Macedo, R. H. (2014). Plumage coverage is related to body condition and ectoparasitism in blue-black grassquits. *The Wilson Journal of Ornithology*, 126, 581-584. https://doi.org/10.1676/13-197.1

Major, R. E., & Kendal, C. E. (1996). The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis*, 138, 298-307. https://doi.org/10.1111/j.1474-919X.1996.tb04342.x

Martin, T. E. (1993). Nest predation and nest sites: new perspectives on old patterns. *BioScience*, 43, 523-532. https://doi.org/10.2307/1311947

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, 65, 101-127. https://doi.org/10.2307/2937160

Martin, T. E., Scott, J., & Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London B: Biological Sciences*, 267, 2287-2293. https://doi.org/10.1098/rspb.2000.1281

McQueen, A., Naimo, A. C., Teunissen, N., Magrath, R. D., Delhey K., & Peters, A. (2017). Bright birds are cautious: seasonally conspicuous plumage prompts risk avoidance by male superb fairy-wrens. *Proceedings of the Royal Society of London B: Biological Sciences*, 284, 20170446. https://dx.doi.org/10.1098/rspb.2017.0446

Menezes, J. C. T., & Marini, M. Â. (2017). Predators of bird nests in the Neotropics: a review. *Journal of Field Ornithology*, 88, 99-114. https://doi.org/10.1111/jofo.12203

Møller, A. P., & Nielsen, J. T. (1997). Differential predation cost of a secondary sexual character: sparrowhawk predation on barn swallows. *Animal Behaviour*, 54, 1545-1551. https://doi.org/10.1006/anbe.1997.9998

Mullin, S. J., & Cooper, R. J. (1998). The foraging ecology of the gray rat snake (*Elaphe obsoleta spiloides*)-visual stimuli facilitate location of arboreal prey. *The American Midland Naturalist*, 140, 397-401. https://doi.org/10.1674/0003-0031(1998)140[0397:TFEOTG]2.0.CO;2

Pagani-Núñez, E., & Senar, J. C. (2016). More ornamented Great tit *Parus major* fathers start feeding their offspring earlier. *Ardea*, 104, 167-176. https://doi.org/10.5253/arde.v104i2.a1

R Core Team. (2018). R a language and environmente for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rangen, S. A., Clark , R. G., & Hobson K. A. (2000). Visual and olfactory attributes of artificial nests. *The Auk*, 117, 136-146. https://doi.org/10.1642/0004-8038(2000)117[0136:VAOAOA]2.0.CO;2

Reneerkens, J., Piersma, T., Damsté, J. S. S. (2005). Swtich to diester preen waxes may reduce avian nest predation by mammalian predators using olfactory cues. *Journal of Experimental Biology*, 208, 4199-4202. https://doi.org/10.1242/jeb.01872

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology*, 1-48. https://doi.org/10.5479/si.00810282.9

Santisteban, L., Sieving, K. E., & Avery, M. L. (2002). Use of sensory cues by fish crows *Corvus ossifragus* preying on artificial bird nests. *Journal of Avian Biology*, 33, 245-252. https://doi.org/10.1034/j.1600-048X.2002.330306.x

Skutch, A. F. (1949). Do tropical birds raise as many young as they can nourish? *Ibis*, 91, 430-455. https://doi.org/10.1111/j.1474-919X.1949.tb02293.x

Skutch, A. F. (1985). Clutch size, nesting success, and predation on nests of tropical birds, reviewed. *Ornithological Monographs*, 36, 575-594. https://doi.org/10.2307/40168306

Slagsvold, T., Dale, S., & Kruszewicz, A. (1995). Predation favours cryptic coloration in breeding male pied flycatchers. *Animal Behaviour*, 50, 1109-1121. https://doi.org/10.1016/0003-3472(95)80110-3

Snow, D. W. & Snow, B. K. 1964. Breeding seasons and annual cycles of Trinidad land birds. *Zoologica*, 49, 1-39.

Söderström, B. (1999). Artificial nest predation rates in tropical and temperate forests: A review of the effects of edge and nest site. *Ecography*, 22, 455-463. https://doi.org/10.1111/j.1600-0587.1999.tb00582.x

Stake, M. M., Thompson III, F. R., Faaborg, J., & Burhans, D. E. (2005). Patterns of snake predation at songbird nests in Missouri and Texas. *Journal of Herpetology*, 39, 215-222. https://doi.org/10.1670/150-04A

Stuart-Fox, D. M., Moussalli, A., Marshall, N. J., & Owens, I. P. F. (2003). Conspicuous males suffer higher predation risk: visual modeling and experimental evidence from lizards. *Animal Behaviour*, 66, 541-550. https://doi.org/10.1006/anbe.2003.2235

Stuart-Fox, D. M., & Ord, T. J. (2004). Sexual selection, natural selection and evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London B: Biological Sciences*, 271, 2249-2255. https://doi.org/10.1098/rspb.2004.2802

Stuart-Fox, D., & Moussalli, A. (2008). Selection for social signalling drives the evolution of chameleon colour change. *Plos Biology*, 6, e25. https://doi.org/10.1371/journal.pbio.0060025

Sundberg, J., & Larsson, C. (1994). Male coloration as an indicator of parental quality in the yellowhammer, *Emberiza citrinella*. *Animal Behaviour*, 48, 885-892. https://doi.org/10.1006/anbe.1994.1313

Thompson III, F. R. (2007). Factors affecting nest predation on forest songbirds in North America. *Ibis*, 149, 98-109. https://doi.org/10.1111/j.1474-919X.2007.00697.x

Weatherhead, P. J., & Boag, P. T. (1995). Pair and extra-pair mating success relative to male quality in red-winged blackbirds. *Behavioral Ecology and Sociobiology*, 37, 81-91. https://doi.org/10.1007/BF00164153

Weatherhead, P. J., & Blouin-Demers, G. (2004). Understanding avian nest predation: Why ornithologists should study snake. *Journal of Avian Biology*, 35, 185-190. https://doi.org/10.1111/j.0908-8857.2004.03336.x

Whelan, C. J., Dilger M. L., Robson, D., Hallyn, N., & Dilger S. (1994). Effects of olfactory cues on artificial-nest experiments. *The Auk*, 111, 945-952. https://doi.org/10.2307/4088826

Yasukawa, K. (2017). Nest defense by male Red-Winged Blackbirds (*Agelaius phoeniceus*) improves survival of broods they provision. *The Journal Wilson of Ornithology*, 129, 368-372. https://doi.org/10.1676/16-086.1

Yezerinac, S. M., & Weatherhead, P. J. (1997). Extra-pair mating, male plumage coloration and sexual selection in yellow warblers (*Dendroica petechia*). *Proceedings of the Royal Society of London B: Biological Sciences*, 264, 527-532. https://doi.org/10.1098/rspb.1997.0075

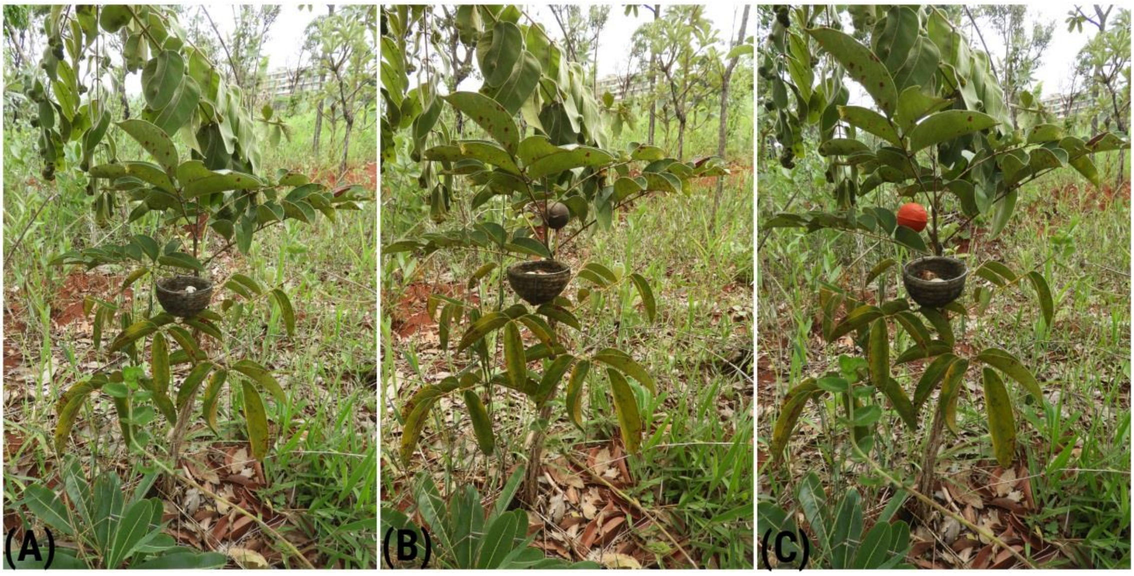
Zahavi, A. (1975). Mate selection-A selection for a handicap. *Journal of Theoretical Biology*, 53, 205-214. https://doi.org/10.1016/0022-5193(75)90111-3

Table 1. Observed rates of nest predation (%) and results of chi-square test comparisons between control and treatment groups. In hypothesis 1, control group (82 nests) without visual cue (parental absence) and treatment (164 nests) with visual cue (parental presence). In hypothesis 2, 82 nests for each group being control group with presence of cryptic (brown) parent and treatment with presence of conspicuous parent (red).

	Hypothesis 1		Hypothesis 2	
	Predation Level	Chi-square test	Predation Level	Chi-square test
Treatment	12.19	$X^2 = 0.004$	9.75	$X^2 = 0.512$
Control	10.97	$p = 0.944$	14.63	$p = 0.474$

Figure legend

Figure 1. Nests of experiment carried out in this study: (a) Control group without “parental” presence; (b) treatment nest simulating presence of a cryptic “parent”; and. (c) treatment nest simulating presence of a conspicuous parent.



CONCLUSÃO GERAL

A predação e o parasitismo de ninhos são uma poderosa força seletiva capaz de moldar vários comportamentos e atributos da história de vida das aves. Neste trabalho observarmos que, de forma sinergética, ambos os fatores podem aumentar ainda mais o insucesso reprodutivo das aves. Ovos ejetados aumentaram a taxa de predação de ninhos e são, portanto, mais um obstáculo no desenvolvimento de estratégias antiparasitismo. Ao ejetar um ovo, hospedeiros podem comprometer toda sua ninhada ao atraírem mais predadores de ovos. Isso explica por que muitas vezes o parasitismo de ninhada ultrapassa estágios iniciais como, incubação e eclosão e muitos hospedeiros não ejetam ovos mesmo quando conseguem diferenciar entre seus filhotes e o do parasita. Estudos futuros devem procurar se essa relação permanece para espécies com diferentes tipos de comportamento de rejeição como, *grasp-ejection,* o hábito do hospedeiro carregar o ovo segurando-o inteiro no bico e *puncture ejection* o hábito do hospedeiro perfurar o ovo com o bico para então carrega-lo para fora do ninho.. Além disso, avaliar diferentes alturas do ninho também pode auxiliar a compreender se a ejeção de ovos pode influenciar a taxa de predação de ninhos em diferentes sítios de nidificação.

Em relação à influência de pistas na taxa de predação de ninhos, os resultados foram bem contrastantes. Enquanto pistas olfativas aumentaram a taxa de predação no primeiro estudo, pistas visuais parecem não fazer efeito na taxa de predação. Esse resultado se mostra bastante robusto ao ser encontrado em estudos diferentes em anos diferentes. Isso remete ao fato de que os predadores dessa área sejam orientados pelo olfato, como pequenos mamíferos. Ao buscar relação entre conspicuidade e predação, também não foi encontrado aumento na taxa de predação. Entretanto, cabe destacar aqui, que, experimentos com ninhos artificiais carecem de diversos atributos dos parentais que influenciam diretamente a taxa de predação. Enquanto diversos estudos relatam uma maior taxa de predação nos trópicos, pouco ainda se sabe sobre como a predação pode influenciar a resposta de suas presas em algumas áreas. Sendo assim, mais estudos com predação de ninho nessas áreas são necessários para identificar quem são os predadores dessas áreas e quais mecanismos sensoriais são usados para encontrar suas presas.