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UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA

HORIZONTAL TRANSFER, GEOGRAPHIC DISTRIBUTION AND SPECIATION IN FEATHER MITES IN BRAZIL (ASTIGMATA)

TRANSFERÊNCIA HORIZONTAL, DISTRIBUIÇÃO GEOGRÁFICA E ESPECIAÇÃO EM ÁCAROS DE PENAS NO BRASIL (ASTIGMATA)

LUIZ GUSTAVO DE ALMEIDA PEDROSO

Rio Claro – SP

2022

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Transferência horizontal, distribuição geográfica e especiação em ácaros de penas no Brasil (Astigmata)

Horizontal transfer, geographic distribution and speciation in feather mites in Brazil (Astigmata)

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Zoologia.

Orientador: Prof. Dr. José Paulo Leite Guadanucci

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Coorientador: Prof. Dr. Almir Rogerio Pepato

Rio Claro – SP

2022

P372t

Pedroso, Luiz Gustavo de Almeida
Transferência horizontal, distribuição geográfica e especiação em ácaros de penas no Brasil (Astigmata) / Luiz Gustavo de Almeida Pedroso. -- Rio Claro, 2022
145 p.

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro
Orientador: José Paulo Leite Guadanucci
Coorientador: Fabio Akashi Hernandes, Almir Rogerio Pepato

1. Acariformes. 2. Ave. 3. Simbiose. 4. Filogenia. 5. Hospedeiro. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências, Rio Claro. Dados fornecidos pelo autor(a).

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TÍTULO DA TESE: Transferência horizontal, distribuição geográfica e especiação em ácaros de penas no Brasil (Astigmata)

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Rio Claro, 13 de junho de 2022

Dedico essa obra às mais de 600.000 vítimas da COVID-19 no Brasil.

Agradecimentos

Primeiramente, à FAPESP – Fundação de Amparo à Pesquisa do Estado de São Paulo (Processos 2016/11671-1 e 2018/21504-0), pela oportunidade. Esse projeto não seria possível sem o financiamento da mesma. Aqui agradeço também a CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, pelo fomento indireto através do financiamento da pós-graduação brasileira, que sustenta o país na décima terceira colocação em produção científica mundial, mesmo apesar dos percalços dos últimos anos.

Os primeiros anos desse projeto foram de muita apreensão, principalmente devido ao cenário político do país, que desde 2016 causava incertezas sobre o futuro da carreira científica. Incertezas essas que se mostraram ainda piores nos anos seguintes, não apenas devido à pandemia, que nos enclausurou, mas também pela ascensão de um dos piores governos da história do país. Esse doutorado termina num ano derradeiro para o futuro do país. Seguiremos lutando.

Gostaria de agradecer a meu orientador, Dr. Fabio Akashi Hernandes, que primeiramente me incentivou na escrita e submissão do projeto desse doutorado, e que, depois de aceito pela FAPESP, topou me orientar mesmo sabendo que sua estadia pela UNESP de Rio Claro estava próxima do fim (por um ótimo motivo, diga-se de passagem!). Foi ele quem primeiramente me introduziu nessa saga pelo conhecimento e entendimento dos ácaros de penas, essas formas de vida tão peculiares. Dessa vez, porém, por um caminho até então não explorado por nós – o das análises ecológicas e moleculares.

Os agradecimentos seguem quanto à necessidade de analisar as aves para a coleta dos ácaros, tanto vivas, capturadas com redes de neblina, quanto em peles ornitológicas de coleções em museus. Portanto, aqui agradeço os curadores das coleções ornitológicas em museus por permitirem meu acesso para a coleta desses ácaros: Prof. Dr. Glayson Ariel Bencke, do Museu da Fundação Zoobotânica de Porto Alegre (MCN, Porto Alegre, Rio Grande do Sul); Prof. Dr. Carla Suertegaray Fontana, do Museu de Ciências e Tecnologia da PUC (MCT, Porto Alegre, Rio Grande do Sul); Antenor Silva Junior e Ma. Patrícia Weckerlin e Silva, do Museu de História Natural Capão da Imbuia (MHNCI, Curitiba, Paraná); Prof. Dr. Luis Fábio Silveira, do Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, São Paulo); e Prof. Dr. Alexandre Aleixo, do Museu Paraense Emílio Goeldi (MPEG, Belém, Pará). E aos professores das Universidades as quais realizei a captura (ou abdução!) de aves com redes de neblina, acompanhado de alunos ajudantes, que incluem

a Prof. Dr. Gerturd Müller e a sua aluna Prof. Dr. Fabiana F. Bernardon, na UFPel (Pelotas, RS); a Prof. Dr. Lilian Manica e seu aluno Rafael Fratoni na UFPR (Curitiba, PR); ao Prof. Dr. Luiz dos Anjos e sua aluna Larissa C. Calsavara na UEL (Londrina, PR); ao Prof. Dr. Edson Guilherme da Silva e suas alunas, Ma. Luana Alencar e Vanessa Lima de Souza, na UFAC (Rio Branco, Acre); ao Prof. Dr. Mauro Pichorim e sua aluna Amanda na UFRN (Natal, RN); ao Dr. Luciano Naka e seu aluno Victor na UFPE (Recife, PE); ao Dr. Roberto Cavalcanti, na UNB (Brasília, DF); ao Prof. Dr. Sérgio Posso, na UFMS (Três Lagoas, MS); e, finalmente, ao Prof. Dr. Marco A. Pizo e seus alunos, que constantemente mantém atividades de anilhamento na UNESP de Rio Claro, em especial ao Ivan Provinciato, Caroline Toledo, André L. B. Moraes, e Dr. Augusto F. Batisteli. A coleta de todo esse material me permitiu vivenciar experiências únicas, conhecer pessoas e lugares muito especiais. Deixo aqui meu muito obrigado. Também agradeço ao Prof. Dr. Miguel Ângelo Marini, o encontrei num primeiro momento no MZUSP, e quando o encontrei de novo, na UNB, recebi de presente exemplares físicos do "*Feather Mites of the World*", a bíblia dos ácaros de penas. Grande presente!

Com o material coletado, a próxima etapa seria a extração e sequenciamento do material genético desses ácaros. Aqui entram o Prof. Dr. Almir Rogerio Pepato e sua equipe na UFMG, Brenda e Samuel, pela grande ajuda me mostrando como realizar a extração de DNA e os procedimentos para PCR em Acariformes. A UFMG e o Almir, a princípio, estavam nos meus planos de possível lugar para a realização do doutorado, não fosse o aceite da FAPESP. Almir também foi a ponte depois para meu contato com o Dr. Pavel B. Klimov, até então da Universidade de Michigan, onde realizei toda a parte molecular desse projeto. Aqui fica, então, toda minha gratidão ao Pavel, o qual me ajudou não só com a parte molecular, mas também deu suporte para as análises estatísticas, filogenéticas, revisão crítica, e escrita do manuscrito principal. Ainda em Michigan, não posso deixar de lembrar e agradecer todo pessoal do RMC (Research Museum Center), em particular ao Micheal Wynne, com o qual tomávamos café todas as manhãs religiosamente, grande Mike! Agradeço também ao Dr. Barry M. OConnor, uma lenda da acarologia que tive a honra de conhecer pouco antes de se aposentar. E ao Sergei Mironov, o atual "*pai dos ácaros de pena*", o qual além de ter doado amostras essenciais ao projeto, também é sempre solicito em ajudar e faz revisões de forma muito paciente e cordial.

Por fim, agradeço ao meu orientador de adoção, Prof. Dr. José Paulo L. Guadanucci. Ele me adotou quando Fabio se mudou para UFSC. Sou para ele quase o que um filhote de chupim é para sua ave hospedeira, no qual eu o parasito pedindo assinaturas burocráticas. Valeu, Zé!

Agora a parte de coração (não que os outros não sejam!). Agradeço minha mãe, com quem venho me conectando cada vez mais, e que além do suporte emocional me ajudou a organizar minha viagem para o Congresso Internacional de Acarologia na Turquia. Agradeço ao meu irmão Lucas, por sempre me ajudar quando preciso, e aos meus amigos, Rafael (da Dinamarca, o bff), Rafael (da Botânica), Rafael (de Bauru), e Rafael (o Pinas), quantos Rafaéis! A galera de Bauru: Edwin, Mario, Iago, Jubas. Aos amigos da minha antiga Rep. Tassio e Ana e agregados. A companheira de rolês e aulas de inglês Giullia. O pessoal do LARC: Hector (pelos cafés e rolês gastronômicos), Wolf (ajudou a limpar as lentes fungadas dos equipamentos pós-pandemia!), Arthur (pela ajuda com o fim do doc), Victor (quase morremos indo pro simpósio na UFMG), e outras tantas pessoas que aqui não marquei, mas que de alguma forma foram essenciais nessa etapa da minha vida. Agradeço por último uma das pessoas mais importantes, Douglas, que hoje é meu companheiro e foi fundamental para que eu conseguisse suportar (ainda estou suportando) a barra mental que muitas vezes é fazer pesquisa.

Muito obrigado a todos vocês!

RESUMO

A especificidade é um aspecto crucial que governa as interações entre simbiontes e hospedeiros. Geralmente a especificidade está ligada ao potencial de transmissão, à plasticidade adaptativa, e à disponibilidade de hospedeiros de simbiontes. Apesar da importância, a especificidade ainda é um assunto complexo em muitos sistemas simbionte-hospedeiro, especialmente quanto ao potencial de simbiontes emergirem em novos hospedeiros. Ácaros de penas (Astigmata: Analgoidea e Pterolichoidea) são exemplos de simbiontes altamente específicos. Por serem ectosimbiontes obrigatórios e de aparente baixa mobilidade, a transmissão em ácaros de penas ocorre de maneira íntima no contato entre hospedeiros. Ocorrendo primeiramente verticalmente, dos genitores para seus descendentes, durante o desenvolvido cuidado parental das aves. Acredita-se que a transmissão vertical seja um fator chave responsável pela alta especificidade observada em ácaros de penas, onde muitas espécies de ácaros são encontradas apenas em espécies intimamente relacionadas. Portanto, sistemas que alteram os padrões de transmissão de ácaros de penas oferecem uma oportunidade valiosa de investigação da relação entre transmissão, especificidade, e distribuição geográfica. Aqui entra o chupim (*Molothrus bonariensis*), uma ave nidoparasita generalista que depende de outras espécies de aves para encubar seus ovos e cuidar de seus ninhegos, o que impede a transferência vertical intraespecífica de ácaros de penas. Não é surpresa que esse sistema ainda não tenha sido estudado, já que o conhecimento sobre ácaros de penas ainda é incipiente na região neotropical. Portanto, aqui investigamos a fauna de ácaros de penas do chupim e de seus hospedeiros potenciais no Brasil. A presente tese se divide em duas partes principais: a primeira parte foca em inventariar ácaros de penas do chupim e busca entender como os ácaros encontrados se relacionam com a especificidade e a transmissão nesse sistema; a segunda parte foca na distribuição geográfica desses ácaros de penas no Brasil, também buscando correlacionar a especificidade. Por múltiplas linhas de evidência (abundância, prevalência, filogenia e cofilogenia) foi possível diferenciar ácaros específicos do chupim de ácaros adquiridos verticalmente de aves por ele parasitadas. Com base nessas diferenças foi possível estimar taxas de transmissão vertical e horizontal nesse sistema. Mesmo sem possuir transmissão vertical de ácaros de penas, o chupim apresentou uma fauna de ácaros específicos diversa, composta por cinco espécies em cinco gêneros. Essa especificidade é mantida por transferências horizontais intraespecíficas, estimadas a serem pelo menos três vezes maiores que do que as taxas de transmissão vertical. Extrapolando para outros sistemas, a transmissão vertical de ácaros de penas, ainda no ninho, é importante para uma primeira aquisição desses simbiontes, porém a transmissão horizontal é provavelmente a principal responsável pela difusão desses ácaros nas populações de seus hospedeiros. Quanto a padrões de distribuição, por análises de modulação geográfica foi possível identificar que a distribuição da fauna de ácaros não específicos no chupim segue padrões de preferências de uso de seus hospedeiros. Foi possível também corroborar a eficiência da transmissão horizontal em manter uniforme a distribuição de seus ácaros específicos. Por fim, são mostrados padrões de distribuição geográfica em ácaros de penas em diferentes populações de hospedeiros de ampla distribuição no Brasil, com potenciais espécies crípticas. Novas espécies de ácaros de penas também foram descritas. As descobertas e novidades aqui

trazidas contribuem para um novo entendimento sobre a dispersão e organização de ácaros de penas em seus hospedeiros, comprovando um maior padrão de eficiência de transferências horizontais até então não estimado para o grupo. Os dados também indicam um papel fundamental da especificidade como fator limitante da distribuição geográfica e da colonização de novos hospedeiros por esses simbiontes.

Palavras-chave: Acariformes, Ave, Simbiose, Filogenia, Hospedeiro

ABSTRACT

The specificity is a crucial aspect ruling host-symbiont interactions. It is usually linked to the symbiont's transmission potential, adaptation plasticity, and availability of compatible hosts. Despite its importance, specificity is still a complex subject in many host-symbiont systems, especially regarding their potential to emerge into new hosts. Feather mites (Astigmata: Analgoidea and Pterolichoidea) are examples of such highly specific symbionts. Because of their obligatory association and apparent low mobility, their transmission occurs by intimate contact between avian hosts, usually through vertical transmission from parents to offspring. This vertical transmission is believed to be a key factor sustaining the high host specificity in feather mites, as many mite species are found solely on closely related hosts. Systems disrupting this transmission pattern offer valuable opportunities to investigate host specificity and other aspects of feather mite biology, such as geographic distribution. Here enters the shiny cowbird (*Molothrus bonariensis*), a brood parasitic bird that relies on other passerines to rear their chicks, preventing the usual vertical transmission of feather mites. It is no surprise that this system has never been studied as the knowledge of feather mites in the Neotropical region is still incipient. Therefore, here we investigate the feather mite fauna on the shiny cowbird and their most common hosts in Brazil. The present thesis is divided into two main subjects: a first part focused on recording the feather mite fauna from the shiny cowbird and understanding their relationship with aspects of host specificity and transmission; and a second part focused on the geographic distribution of feather mites in Brazil, also connecting it to host specificity properties. By multiple lines of evidence (abundance, prevalence, phylogenetic, and co-phylogenetic), it was possible to differentiate specific-to-cowbird mites from mites acquired from their foster parents and estimate rates of vertical and horizontal transmission in this system. Even lacking vertical intraspecific transmission, the shiny cowbird presented a diverse feather mite fauna composed of five species in five genera. This specific fauna is only transmitted horizontally, which occurs at a rate three times higher than vertical transmissions. Estimating for other systems, the vertical transmission of feather mites is important for a primary acquisition of these symbionts, while the horizontal transmission is likely the main responsible for the dispersal of these mites on host populations. Regarding their distribution, modularity analyzes identified patterns of distribution for the non-specific mites on shiny cowbirds explained by their preferences in host usage in different regions. It was also possible to corroborate the efficiency of horizontal transmissions in keeping their specific mite fauna evenly distributed in Brazil. Finally, patterns of the geographic distribution of feather mites on different host populations are shown in Brazil, with potential cryptic species. New feather mite species were also described. The novelties in the present work collaborate to understand the dispersion and organization of feather mites on their hosts, acknowledging a higher efficiency of horizontal transmissions than expected in these apparently low mobile symbionts. Our data also reinforce the importance of the host specificity as the limiting factor for the distribution and the colonization of new hosts by feather mites.

Keywords: Acariformes, Bird, Symbiosis, Phylogeny, Host

SUMMARY

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INTRODUCTION

GENERAL INTRODUCTION

Taxonomic concepts – what are feather mites?

Among the vastly diverse arthropod Subphylum Chelicerate, an expressive variety of the Arachnida Subclass Acari (mites) developed adaptations to fully or partially live in association with birds (Aves). These adaptations allowed mites to exploit nearly all possible habitats and microhabitats offered by these hosts, which in birds include their nesting sites, their external appendages (i.e., feathers), inside the quill of feathers, the superficial and subcutaneous layers of their skin, and reaching as deep as inside their respiratory tract and visceral tissues. This diversity of bird-associated mites sums more than 3,000 described species in at least 40 families (Knee et al. 2008), representing around 5.5% of all named mite diversity in the world, an astonishing number if we consider Acari as one of the most diverse metazoan groups with more than 54,000 named species (Beaulieu et al. 2019; Walter & Proctor 2013). Simultaneously, Acari is also one of the least known clades, with nearly 1 million species estimated in the group, which highlights the still long path to building a solid Acari knowledge.

Traditionally Acari is recognized as a monophyletic Subclass divided into two large Superorders – Parasitiformes and Acariformes. The Acari monophyly is, however, up to debate due to contrasting topologies in molecular phylogenetic studies, sometimes placing Acariformes more related to other Arachnida Orders such as Solifugae or Pseudoscorpiones than to Parasitiformes (Arribas et al. 2020; Dabert et al. 2010; Lozano-Fernandez et al. 2019; Pepato & Klimov 2015; Sharma et al. 2014). Debates aside, bird-associated Acari are found on both Superorders. Noteworthy bird-associated Parasitiformes include the Order Ixodida of soft (Argasidae) and hard ticks (Ixodidae), and the Order Mesostigmata, with the red mites (Dermanyssidae), the nasal mites (Rhinonyssidae), and the fowl mites (Macronyssidae), all of medical and veterinary importance (Bassini-Silva et al. 2019; Camargo-Mathias et al. 2020; Hilario-Pérez & Dowling 2020; Ogrzewalska & Pinter 2016). However, the vast majority of bird-associated mites are, however, in the Superorder Acariformes – also known as the "mite-like mites" (Walter & Proctor 2013). Acariformes further split into two major Orders, the Trombidiformes, which in association with birds includes the Suborder Prostigmata; and the Sarcoptiformes, represented on birds by the Suborder (or Hyporder) Astigmata (Krantz & Walter 2009; Mullen & OConnor 2019). The most common bird-associated Prostigmata are the quill mites of the family Syringophilidae, followed by the chiggers (Trombiculidae), and

the harpirhynchine mites (Harpirhynchidae) – all true parasites that feed on their host's fluids (e.g., blood, lymph) (Bochkov et al. 2015; Fain et al. 2002; Jacinavicius et al. 2018; Mullen & OConnor 2019; Skoracki et al. 2013). Astigmatan mites, on the other hand, are well-known as one of the most diverse mite groups to live in association with vertebrate hosts (Krantz & Walter 2009; OConnor 1982; Walter & Proctor 2013). On birds, Astigmata includes some of the most strikingly specialized mites, such as the quill wall mites (Laminosioptidae), the invasive visceral mites (deutonymphs of Hypoderatidae), and the nasal cavity mites (Tubinoptidae, Cytoditidae, Gastronyssidae, and Ereynetidae) (Beaulieu et al. 2019).

Remarkably, The most impressive diversity of mites on birds is the so-called "feather mites" from the Superfamilies Analgoidea and Pterolichoidea, with around 2,600 named species (Gaud & Atyeo 1996; Hernandes 2021). The former Superfamily Freyanoidea of feather mites, presented in a complete feather mite catalog to date done by Gaud and Atyeo (1996) – "Feather mites of the World", is now considered nested inside Pterolichoidea by the majority of feather mite taxonomists following OConnor (1982) (Mironov 2003). The Analgoidea and Pterolichoidea, together with the mammal-specialized mites of the Superfamily Sarcoptoidea, form the monophyletic supercohort of symbiotic-mites Psoroptidia (Bochkov 2011; Klimov & Oconnor 2013; Mironov 2003). Therefore, the term "feather mites" referring to the Superfamilies Analgoidea and Pterolichoidea is phylogenetically artificial since molecular studies have placed Sarcoptoidea mites (mammals-only symbionts) inside the traditionally bird-only Analgoidea. In this regard, solely the around 15 families of avian mites in Analgoidea presented in Gaud and Atyeo (1996) are considered to be part of the "true feather mite" group along with Pterolichoidea (Gaud & Atyeo 1996; Klimov & Oconnor 2013). In addition, many experts also recognize the possibility of Analgoidea and Pterolichoidea to be a diphyletic group derived from different psoroptidian lineages, emphasizing the paraphyly in feather mites and the ecological restriction to the term "feather mite" (Mironov 2003). Moreover, it is noteworthy that by following Gaud and Atyeo (1996) classification, Analgoidea also includes the family Pyroglyphidae. Although this family include some species living in association with bird's feathers, most pyroglyphids live on the nest of their hosts or are free-living mites, which include some medically-important taxa such as house-dust mites (i.e., *Dermoglyphus*) responsible for respiratory allergies in humans (e.g., asthma). This taxonomic relationship was later confirmed in a molecular study that nested the Pyroglyphidae lineage inside the Superfamily Analgoidea of almost exclusive obligate-symbiont mites, indicating the

reversion or loss of this obligatory symbiotic lifestyle towards free-living species, a rare phenomenon (Klimov & Oconnor 2013).

Following the exposed above, the present doctoral thesis follows the feather mite concept presented in Gaud and Atyeo (1996), which includes all the ca. 33 families of obligatory-symbiotic psoroptidian mites associated with almost all modern bird orders. For suprafamilial ranks, this work partially follows the changes proposed by OConnor (1982) in respect of nesting the Superfamily Freyanoidea inside Pterolichoidea, but not regarding his decision to separate pyroglyphid-like mites into a new Pyroglyphoidea Superfamily (Mironov 2003).

Historical background

The knowledge of feather mites formally began in 1758 when the species *Acarus passerinus* was described from the Common chaffinch *Fringilla coelebs* L., 1758 (Fringillidae) by Carl Linnaeus, which today corresponds to the mite species *Analges passerinus* (Linnaeus, 1758) (Analgidae). This first step to building feather mite knowledge was named the "*primary feather mite investigation*" by Mironov (2003). Mironov (2003) also recognized and named other subsequent and important landmarks in the history of the feather mite knowledge, briefly described as follows (Mironov 2003). After Linnaeus, feather mites would receive attention again only at the end of the 19th century (from 1860 to 1920), with additional species descriptions, early taxonomic concepts for suprageneric ranks, and the concept of "feather mite" itself done by pioneers taxonomists and naturalists such as Robin, Trouessart, Neumann, Mégnin, and Oudemans, a period named as "*classical*" in feather mite studies (Mironov 2003). However, the feather mite studies bloomed around 1950 in a monography series dedicated to the group by Dubinin (1951, 1953, 1956). Dubinin settled feather mites as a monophyletic taxon in the Superfamily Analgoidea (as Analgesoidae) for the first time, building the background to feather mite systematics and ecology, a period named "*Renaissance*" in feather mite studies, lasting until 1970 (Gaud & Atyeo 1996; Mironov 2003). During the Renaissance, the most expressive and valuable contributions to feather mite systematics in the 20th century were developed, boosted by studies done by two prominent feather mite enthusiasts – Jean Gaud and Warren T. Atyeo. These authors studied feather mites from early 1950 until 1996. They described and established many new genera, families, and superfamilies of mites (e.g., Pterolichoidea and Freyanoidea) pushed by the crescent taxonomic descriptions (Gaud & Atyeo 1977). Concomitantly, another prominent

acarologist, Alex Fain, also enormously expanded the knowledge of the field, exceptionally for skin mites of the families Dermationidae and Epidermoptidae (Fain 1965).

The advances in feather mite knowledge described above were restricted mainly to African and European taxa by that time. In the Renaissance timeframe, the first efforts to advance the feather mite knowledge in the Neotropical region were expressively made by Berla, in a series of works from 1950 to 1970 describing species from Brazil, and by Černy, describing species from Central America (e.g., Berla 1959; Černý 1974).

The "*Modern*" and last period in the construction of the feather mite knowledge defined by Mironov (2003) goes from the late 1970 and extends up to 2010. This period is marked not only by deeper investigations regarding the superfamilial ranks and new taxonomic concepts (e.g., OConnor 1982) but also by advances in underexplored fields such as feather mite ecology, systematics, and host-symbiont relationships (e.g. Dabert and Ehrnsberger 1999; Blanco et al. 2001). The Modern period can be extended up to the early years of 2010, to include the second wave of advances in feather mite systematics in underexplored regions of the world, exceptionally in the taxonomically rich tropical regions – including Brazil (e.g., Faccini et al. 1976; Valim and Hernandes 2008; Hernandes et al. 2010; Valim et al. 2011). This increased taxonomic effort overtime was responsible to named around 25% (ca. 2,600 species) of the total feather mite diversity estimated to the group globally, taking into account that each bird species (from around 10,000) can host multiple highly specific feather mite species due to microhabitat repartition, where even congeneric mites can be found living in synhospitality (i.e., mites sharing the same microhabitat without apparent competition) (Bochkov & Mironov 2008; Walter & Proctor 2013).

Herein I include a new phase to the feather mite knowledge timeline: the "*Contemporary*" period. This period is needed to embrace the astonishing advances achieved by using molecular data in feather mite studies, which started around early 2010 and extend to the present (Dabert et al. 2010; Knowles & Klimov 2011, but see Dabert et al. 2001). So far, the Contemporary period is giving new and important evidence corroborating earlier assumptions contrary to the general concept of feather mites as motionless symbionts, e.g., by recording multiple cases of historical host switch events in cophylogenetic assessments – also contesting the initial idea of high coevolutionary congruence between mites and birds. These studies also exposed our lack of knowledge regarding the parameters responsible for delimiting the generally high host specificity level in feather mites. It was also during the current time, especially pushed by a set of publications by Jorge Doña and his team, that other substantial advances in feather mite ecology, host interaction, and behavior have

occurred (e.g., Doña et al. 2015, 2018b). The following sections briefly detail these expanded ecological ecological, biological, and phylogenetic aspects of feather mite natural history.

Host-symbiont specialization in feather mites

Pioneers in feather mite studies had already speculated about the prevalence of commensalism over parasitism regarding the impact of feather mites on their host's welfare. The first nominated feather mite genera, *Analges* Nitzsch, 1818, comes from the Greek word *analgēsía*, which means painless, which in turn is a combination of the prefix *an-* (without), and *algéō* (pain), and was likely attributed to this feather mite due to its apparent harmless effect on bird fitness. This innocuous property was later confirmed for the majority of feather mite species, especially those living on the stiff flight and tail feathers, i.e., far from their host's skin, as no correlation was found between the decrease in their host's fitness and the increase of mite abundance (Doña et al. 2018b). In fact, the opposite appears to be accurate, and better host conditions were recorded in high feather mite densities, suggesting a potential mutualistic relationship (Blanco et al. 2001; Dowling et al. 2001; Galván et al. 2012). Their feeding habit explains the commensalism-mutualism in feather mites: feather mites similarly use their chelicera as the movement of a "cloth wiping a sword," going barbule by barbule from the bottom up to capture tiny particles trapped in the uropygial secretions (i.e., preen oil) such as fungi, algae, bacteria, pollen, and other debris in which they feed upon (Doña et al. 2018b). By doing so, they likely prevent the development of potentially detrimental organisms to the bird's health (e.g., keratinophilic organisms) (Doña et al. 2018b). Recently, Labrador et al. (2021) indirectly estimated the cleaning potential of feathers by feather mites by roughly measuring the amount of organic material that each mite can eat from the feathers in a night of feeding. They found that feather mites can yearly clean an area of *ca.* 80,000 m^2 considering all European passerines, reinforcing their role as feather-cleaning agents. There is also the possibility of feather mites feeding on the preen oil that birds spread over their feathers to protect their integrity and give them a waterproof property (Moreno-Rueda 2017). If true, by removing this bioproduct from the feathers, two interpretations may be possible: 1) the mites could potentially help birds by preventing oil accumulation and the growth of pathogenic organisms; 2) the mites may put pressure on their hosts to replace the consumed preen oil, an energetically costly activity to birds (Moreno-Rueda 2017); however, the latter assumptions have never been tested.

Despite the non-detrimental impact of feather mites, especially those specialized to live on flight and tail feathers, some feather mites are undoubtedly parasites. This is the case for some mites living on the down and covert feathers and all mites living on the superficial layers of the skin and inside the quill of feathers (Dabert & Mironov 1999; Mironov 1987). The proper categorization of feather mites by their living microhabitat is fundamental, as it not only shapes the ecological interaction with their hosts, but apparently also affects their transmission, morphology, and evolutionary properties (Dabert et al. 2015). First attempts of mite categorization were done by Dubinin (1951) but properly described later by Mironov (1987) and Dabert and Mironov (1999). Brief descriptions of each category are given as follows.

Mites living on the ventral and dorsal sides of the flight and tail feathers are known as "vane-dwelling mites." Those mites are usually found motionless and organized in rows on the feather's vanes, i.e., the ventral space between the feather's barbs. Morphologically, vane mites usually present an elongated and dorsoventrally flattened body, short dorsal setae, and well sclerotized dorsal shields, which likely protect them from feather abrasion and water loss as they are more exposed to the external environment. The ambulacra, the disc-like "feet" of feather mites, is also more developed in vane mites and acts as a suction cup preventing the mite from being dislodged during their host's flight. The great majority of the feather mite diversity is composed of vane mites. Living on the more exposed flight feathers may be related to a higher rate of transmission between different host species (i.e., host switch) and may explain their higher diversity, as host switch events were found to be an important driver for feather mite speciation (Dabert et al. 2015; Doña et al. 2017b). Due to their exposed location, vane mites are most accessible and most abundant mites collected in feather mite surveys.

Contrarily to vane mites, which have adaptations against water loss and feather abrasion, mites living on the down feathers – also known as "down mites" – usually receive less selective pressure from the external environment. This feature reflects their morphology: down mites usually possess longer dorsal setae and less sclerotized bodies, exceptionally in females. The longer dorsal setae likely improve their navigation among the soft barbules, in which many representatives of down mites are found, grasped by modified spines and apophyses on their first pairs of legs. The parasitic influence of down mite is rare and seems to occur when the mite population on a bird increases abnormally, often in weak, immunosuppressed, and stressed domestic birds, or as a product of host switch, when a bird receives unspecific mites from other bird species (Hernandes et al. 2014). Down mites'

effects on birds include itchy and dermatitis leading to mange (Faleiro et al. 2015). Examples of such effects include the mite *Allopsoroptoides galli* Mironov, 2013, a down feather mite of the family Psoroptoididae recorded to cause severe mange and dermatitis in laying-egg hens in Brazilian farms, responsible for dropping the egg production up to 30% (Mironov 2013; Soares et al. 2016; Tucci et al. 2014). Later on, it was found that this mite was transmitted to chickens from the Guira Cuckoo, *Guira guira* (Gmelin, 1788), a common cuculid in Brazil (Hernandes et al. 2014). This transmission represented a rare case of host switch and the first record of a mite from the family Psoroptoididae on a galliform bird (Mironov 2003). The lack of a previous host adaptation to this novel feather mite was likely responsible for the aggressive parasitic effect on domestic chickens. However, the stress in which the laying hens are submitted on commercial farms should also be taken into consideration, given that other down feather mites more adapted to chickens, especially from the genus *Megninia* (Analgidae), are also a problem in laying-egg hen systems (Faleiro et al. 2015; Horn et al. 2018; Tucci et al. 2005).

Similar to down mites, quill mites often possess longer corporal setae and weak sclerotized bodies since they spend most of their life in a stable habitat – inside the feather quills, only leaving during their larval and nymphal stages to disperse (Dabert & Mironov 1999). Quill mites often possess strong and hypertrophied chelicerae, which they likely use to rip off parts of the feather medulla, upon which they feed (Dabert & Mironov 1999). This feeding habit gives them the parasitic status, as quill mites may weaken the inner feather structure and facilitate its removal. Quill mites are usually rare and difficult to collect, as they require a careful examination of the feather quill.

Other categorically parasitic feather mites are the skin mites, found on the superficial layers of the skin, as its name implies. These mites usually have a smaller size than other feather mites, a flat and round idiosoma, and short legs. Due to affecting the superficial layers of the skin, these mites are often associated with dermatitis and mange in stressed and immune-depressed birds (Fain 1965). Similar to quill mites, skin mites are also among the most challenging feather mites to sample due to their direct attachment to their host skin, being mostly collected from dead hosts by the washing technique (Mironov & Galloway 2002a).

Overall, detecting detrimental effects of feather mites over their hosts is often tricky, even for categorical parasitic mites (i.e., quill and skin mites). Nevertheless, birds display a myriad of antiparasitic behaviors (e.g., grooming, anting, dustbathing, scratching) that are effective in controlling the population of other symbiotic arthropods, especially feather lice

(Phthiraptera: Ischnocera and Amblycera) (Clayton et al. 2015). A similar potential of symbiont control by birds can also be expected to work against feather mites, minimizing the possibility of harmful effects by controlling their load sizes. For example, Atyeo and Gaud (1979) mentioned they had observed white gulls brown in color due to an extremely high mite load in unhealthy hosts unable to beat their wings. However, unlike feather lice, no direct evidence was found about the bird's ability to control feather mites. Likewise, birds are usually well adapted to their symbionts due to a near-linear coevolutionary history, which reduces the virulent effect of their symbionts. Conversely, more virulent effects are often associated with recent-colonized and not-adapted hosts (i.e., host switch), or triggered by disturbed environments or specific conditions, as noted in the few cases reported in the literature (Hernandes et al. 2014; Longdon et al. 2015).

Specificity and transmission

Due to their obligatory symbiotic properties, all feather mite species must be assigned to at least one host species upon its description and eventually add more host species as new records appear. The available data indicates that feather mites display high host specificity levels since many feather mite species are specifically recorded on a single host species or a set of phylogenetically close-related hosts (Doña et al. 2018a). The high host specificity in feather mites is likely connected to their primary mode of host transmission – vertically from parents to offspring during the bird parental care (Doña et al. 2017a; Mironov & Malyshev 2002). This transmission enhances the chance for an inherited line of mite acquisition, creating a historical host-symbiont association that promotes a parallel evolution between the groups, resulting in the observed intimate level of mite specificity and, to some extent, a phylogenetic congruence between feather mites and birds (Mironov et al. 2020). Conversely, multiple cases of host-symbiont phylogenetic dissimilarities have been recorded in feather mites, especially by advances in cophylogenetic studies (Doña et al. 2017b; Klimov et al. 2017; Matthews et al. 2018a). These studies confirmed previous assumptions of historical host switch events along with feather mite's evolution and suggested that non-parental dispersions, i.e., horizontal transmissions, are likely as important as vertical transmissions for feather mite colonization.

Horizontal transmissions occur post the fledgling stage, when birds become independent from parental care and go into direct contact with unrelated hosts, e.g., during mating, territorial defense, grooming, and predation. Due to the outcome, horizontal

transmissions can be classified into two categories: the ones between conspecific hosts, and the ones between different host species (i.e., interspecific). Evidence of conspecific horizontal transmission includes the absence of mites on nestlings of the Red-billed Choughs *Pyrrhocorax pyrrhocorax* Linnaeus, 1758 (Passeriformes: Corvidae) observed by Blanco et al. (1997); instead, the authors detected an increase in mite abundance along with the bird aging, suggesting a conspecific horizontal route of mite acquisition. Similar mite colonization occurs in Australian brushturkeys (Galliformes: Megapodidae) and some brood parasitic birds such as Cuckoos (Cuculiformes: Cuculidae), since these birds present a specific set of feather mite taxa even completely lacking any parental care behavior, therefore preventing conspecific vertical transmissions. These acquisitions of specific mites in birds lacking parental care are solely possible through horizontal contact between infected and non-infected conspecific birds (Atyeo & Gaud 1983a; Lindholm et al. 1998; Proctor & Jones 2004). Notoriously, these cases of strict conspecific horizontal transmissions have been able to maintain a highly specific fauna in those unconventional birds, confronting the traditional view of vertical transmission as the main route responsible for shaping host specificity.

Interspecific horizontal transmissions, on the other hand, appear to be rare and difficult to detect. Birds display a cornucopia of behaviors capable of promoting the interspecific transmission of feather mites, including altruistic interactions such as allopreening, mixed flocking, sharing nesting grounds, sharing dust and water baths, hybridization, adoption, using other bird species' feathers to build nests; as well as antagonistic such as predation, resources defense, and brood parasitism (Dabert et al. 2015; Johnson et al. 2002a; Ottenburghs 2019; Proctor & Jones 2004; Samplonius & Both 2014; Soler 2017). When the association is ephemeral, i.e., the atypical mite survives on a non-specific host just for a short time, the transmitted mite is recognized as a straggler (Doña et al. 2019b; Ròzsa 1993). In a recent study, Doña et al. (2019) recorded cases of straggler feather mites on 84 of 1,130 (7.4%) passerines in Spain, most of the shared mites on hosts with similar body sizes. Straggler mites were also occasionally recorded on birds of prey since some of these birds frequently carry passerine-related mites, although in low densities (Atyeo & Braasch 1966; Philips 2000). If a straggler mite successfully colonizes a new host, i.e., reproducing and dispersing on the new host population, the association becomes classified as a successful host switch event. Recent host switch events may explain the existence of the same mite species on phylogenetically distant hosts (i.e., polyxenous feather mites), such as the mite *Proctophyllodes polyxenus* Atyeo and Braasch, 1966, recorded on

many host species from at least five passerine families (Atyeo & Braasch 1966). Although, some of those multi-host records may consist of complexes of cryptic mite species.

Successful host switch events are complex and still not fully comprehended in feather mites, neither regarding their transmission pathways nor the properties responsible for accommodating high specialized symbionts into new hosts. Host switch records include the case above of mite transmission from Guira-cuckoos to laying-egg hens in Brazil, resulting in a harmful effect on the new non-adapted host (Hernandes et al. 2014). Previous observations of possible host switch cases in feather mites were made by Gaud (1992), who acknowledged the possibility of the chicken mite *Megninia ginglymura* (Mégnin, 1877), also an economically important mite in the poultry industry, to be a product of host switch from its original host, the American wild turkey *Meleagris gallopavo* Linnaeus, 1758. In his work, Gaud (1992) also noted that domestic pigeons, *Columba livia* Gmelin, 1789, were recorded carrying mite species geographically related to the mite fauna found on native pigeons worldwide. Despite the lack of substantial evidence in his study, Gaud (1992) called attention to the more significant dispersal potential in feather mites than expected, given their apparent low mobility. As previously mentioned, historical host switch events were commonly recorded in bird-mite coevolutionary studies also acknowledging this event as an important driver for feather mite speciation (Doña et al. 2017b; Matthews et al. 2018a).

Unlike stragglers, in which the lack of prior adaptation partly explains the failure to colonize a new host, successful host switches likely depend on specific scenarios and conditions. Among these conditions are the frequency of interaction between the different host species (i.e., the exposition frequency), and the features responsible for shaping the selective pressure and the ecological fitting of alien mites into new hosts, such as the niche availability, the host immune response, and the host-symbiont physiological and morphological compatibility (Agosta et al. 2010; Wells & Clark 2019). However, the factors responsible for shaping the host specificity in feather mites are yet to be investigated.

The lack of knowledge regarding the host specificity in feather mites is partly explained by the challenges and difficulties of monitoring live feather mites on their hosts or keeping them alive *in vitro* (see Labrador et al. 2021). For example, their small size (*ca.* 200 to 500 micrometers) constrains some studies attempting to track or manipulate their movements and populations across hosts. For comparison, feather lice (Phthiraptera), also obligate ectosymbionts on birds, have almost tenfold the size (*ca.* 2 to 5 mm in length) of an average feather mite (Clayton et al. 2015). This difference certainly matters when it is necessary to manipulate and monitor feather mites in experiments across different hosts.

Contrary to feather mites, feather lice have been extensively tested for factors responsible to regulate their populations on hosts, including techniques that allow them to be tagged individually (Zohdy et al. 2012). Apparently, the regulation of lice populations is directly connected to their capacity to colonize new hosts, in a way that what regulates them also seems to regulate their specificity (Bush et al. 2019; Clayton et al. 2003, 2015; Tompkins & Clayton 1999). In the case of lice, the feather structure (correlated with host body size), the host coloration (correlated with the lice' ability to hide from host preening), and the host specialization (i.e., the bill shape), are decisive factors for an effective lice population control by birds, meaning that the host grooming pressure is decisive to remove any non-adapted lice (Bush et al. 2019; Bush & Clayton 2018; Clayton et al. 2003). In feather mites, the closest study experimentally testing the transmission and the factors responsible for mite control by birds was done by Tucci et al. (2014), dealing with the aforementioned case of mite transmission from the guira-cuckoo to laying-egg hens in Brazil (Hernandes et al. 2014; Mironov 2013). In this study, the authors experimentally tested the transmission of mites by placing previously infested chickens together with naïve chickens (i.e., free of mites) in the same controlled cages. They verified that those naïve chickens got infected after 7 days and presented the same symptoms (i.e., scaly dermatitis and mange) observed in naturally infected chickens after 15 days. More importantly, the authors observed that the host grooming ability, which is often impaired in laying-egg hens by practices such as beak trimming and confinement in small cages, appeared not to affect the mite population or prevent their harmful symptoms. This suggests that different from the observed in experiments with feather lice, the host grooming behavior has few effects on the feather mite populations and their specificity. There is also the possibility of feather mites being prone to food shortages making the food availability and the mite's potential to feed on different hosts a factor that may limit the interspecific colonization (Labrador et al. 2021).

The connection between transmission and specificity is strongly demonstrated in phoretic-transmitted feather mites. Some feather mite genera, such as the skin mites *Myialges* Trouessart, 1906 and *Promyialges* Fain, 1964, and the down mite genus *Strelkoviacarus* Dubinin, 1953, have been recorded in phoretic association with other bird-associated arthropods, such as hippoboscid flies (Diptera: Hippoboscidae) and feather lice (Philips & Fain 1991). Phoretic feather mites take advantage of the higher dispersion potential of these other bird symbionts and present lower levels of host specificity like them.

Alternatives to test specificity in feather mites

Despite the advances provided by molecular studies, some aspects of feather mite biology remain elusive, especially concerning the aforementioned host specificity. Given the data at hand, which unfolded host switch as an important event shaping the feather mite evolution and driving their diversification, it is surprising that complex host-symbiont systems promoting constant interaction between non-specific hosts, such as the brood parasitism, remain understudied. Brood parasitic birds do not build nests nor display parental care; instead, these birds lay their eggs on other bird species' nests which act as foster parents for the parasitic chick. This creates a scenario that disrupts the conventional conspecific vertical transmission of feather mites, allowing an effective way to investigate themes related to transmission, host switch, and specificity. Brood parasitism is displayed by around 1% of the bird species in the world (ca. 100 sp.), a behavior which evolved independently seven times in the bird lineage: thrice on cuckoos, represented by the old world tribes Cuculini and Phaenicophaeini, and the new world tribe Neomorphini; once in honeyguides (Piciformes: Indicatoridae); twice on passerines represented by the African whydahs and indigobirds (Passeriformes: Viduidae), and by the new world cowbirds *Molothrus* Swainson, 1832 (Passeriformes: Icteridae); and once in ducks, represented by a single species of duck in South America (Anatidae) (Lowther 2019; Soler 2017; Stevens 2013). The implications for the feather mite diversity in this three-level host-symbiont system (Vas et al. 2013), composed of the brood parasitic bird, the birds they parasitize, and their mites, are virtually unknown, despite their valuable and unique potential to collaborate fundamental understanding questions about the transmission and specificity in feather mites.

The first study concerning feather mites on brood parasitic birds was a review done by Atyeo and Gaud (1983). The authors acknowledged the potential of unspecific mite transmission by foster parents to brood parasitic chicks during parental care. The authors also listed the known mite fauna on each brood parasitic host group, comparing the mite records with their bird hosts and pointing to potential evidence for mite transmission and acquisition. The authors mentioned the record of the mite family Proctophyllodidae on brood parasitic honeyguides of the genus *Prodotiscus* Sundevall, 1850 (Piciformes: Indicatoridae), which brood parasitize passerines, as the most relevant example of potential mite acquisition during parental care from foster parents. Mites of the family Proctophyllodidae are commonly found on Passeriformes, whereas mites recorded on non-brood parasitic honeyguides are mostly the ones typically found on other birds of the order Piciformes, which evidences the potential

mite acquisition and successful host switch from their passerine hosts to honeyguides. Concerning the other brood parasitic bird species, the few records allowed the authors to speculate on the colonization of phylogenetically compatible mites (i.e., not from foster parents) after the post-fledgling stage, especially in cuckoos, since no mites from their typical bird-hosts were recorded.

Another important contribution to the knowledge of feather mites on brood parasitic birds was done by Lindholm et al. (1998), which investigated the transmission of ectosymbionts from passerine foster parents to the diederik cuckoo *Chrysococcyx caprius* (Boddaert, 1783) (Cuculiformes: Cuculidae) in South Africa. In this study, Lindholm et al. (1998) recorded typical passerine mites on nestling cuckoos, an indicative of a vertical pathway of mite transmission during parental care. Notwithstanding, the finding of the mite *Pteronyssoides passeris* (Gaud, 1953) (Analgoidea: Pteronyssidae) on an individual adult cuckoo also indicated some level of mite persistence, as this was a common mite recorded on their passerine hosts. Finally, adult cuckoos also presented a predominant fauna of mites specific to cuckoos, indicating an expressive acquisition of cuckoo mites after leaving their foster parent's nest, likely by conspecific contact. This study provided the first evidences of transmission and persistence of foster parent mites in cuckoos, representing an important finding of host switch between phylogenetically distant related hosts: from Passeriformes to Cuculiformes. Since this study, no other brood parasitic system has been investigated regarding their feather mites. The diederick cuckoo is, therefore, the sole brood parasitic system truly investigated for feather mites and their vertical transmission.

The absence of records of mites acquired from foster parents on other vastly explored cuckoo species, such as the common cuckoo *Cuculus canorus* Linnaeus, 1758, is intriguing, and possibly indicates an incompatibility barrier of colonization still unknown in these symbionts. The knowledge of feather mites on brood parasitic birds phylogenetically closer to their hosts would certainly provide valuable answers and new perspectives on interspecific mite colonization. Whydahs and cowbirds are strong candidates in this category – both represent Passeriformes which parasitize other Passeriformes. They differ by their level of specialization: most whydahs show high levels of host specialization, in many cases parasitizing a single host species, especifically passerines of the family Estrildidae – a sister family to Viduidae (Sorenson et al. 2004); while cowbirds (*Molothrus* spp.) are among the most generalist species of brood parasitic birds, being the shiny cowbird, *Molothrus bonariensis* (Gmelin, 1789), the most generalist of them (Lowther 2019). In this perspective, the shiny cowbird may be one of the best organism models to investigate the potential for

interspecific mite transmission and their settlement on new hosts, as this system is under constant pressure for the colonization by multiple non-specific feather mite species (from the multiple shiny cowbird host species). This adaptation plasticity pressure is a key feature to understand a symbiont's potential to emerge into new hosts (Araujo et al. 2015). Notwithstanding, the shiny cowbird network by itself provides an unmeasurable opportunity to investigate how feather mites adapt to complex systems.

Shiny cowbirds' eggs have been recorded in more than 270 bird species' nests, from which 97 have been recorded successfully rearing their chicks (Fiorini et al. 2019; Lowther 2019; Soler 2017). Natural from the South America Pampas, this species has been spreading its geographical range due to deforestation, being nowadays recorded in all South American countries, the West Indies, and certain North American regions (Cavalcanti 1988; Crespo-Pérez et al. 2016; Levy 2019; Marín 2000; Post et al. 1993; Sick 1997; Sykes Jr & Post 2001). From where it passes, the shiny cowbird is known to reduce its host population, decreasing their reproductive success (Astié & Reboreda 2006; Ortega et al. 2005; Sick 1997; Tuero et al. 2007). Its impact is exceptionally a concern to threatened species such as the yellow-shouldered blackbird *Agelaius xanthomus* (Sclater, 1862) (Passeriformes: Icteridae) in Puerto Rico, and the pale-headed bush-finch *Atlapetes pallidiceps* (Sharpe, 1900) (Aves: Passerellidae) in Ecuador (Azpiroz 2015; Cruz et al. 2005; Lowther 2019; Oppel et al. 2004; Smith et al. 2002). Regarding their symbionts, the shiny cowbird counts with few and sparse studies of feather lice, nasal mites, and helminths (Bernardon et al. 2016; Cicchino & Castro 1996; González-Acuña et al. 2006). For feather mites, there is two described species, the pterodectine *Amerodectes molothrus* (Mironov, 2008) and the proctophyllodine *Proctophyllodes molothrus* Pedroso and Hernandes, 2021, both from Brazil, and recent records of two other species of *Proctophyllodes* from Chile (Mena et al. 2020; Mironov et al. 2008). Therefore, deeper investigations of symbionts on shiny cowbirds, especially their feather mites, are needed for a proper inference of mite specificity and transmission.

Specificity and biogeography – a relationship?

When investigating the specificity of symbionts, another crucial feature must be considered – their geographic distribution (*i.e.*, their biogeography). This consideration is essential for obligate symbionts that complete their entire life cycle on a single host individual; such are feather mites. In these permanent attachment systems, symbionts' geographic distribution usually mirrors their host's distribution. This appears to be the case

for most symbionts on geographically restricted hosts (e.g., endemic species); whereas in locally widespread or ubiquitous hosts (i.e., spread host populations), other factors such as climate variables, host ecology, dispersion potential, and natural barriers might be more relevant than the host to define their distribution (Wells & Clark 2019). Knowing the biogeography of symbionts is also an indirect way to give insights into their host's biogeography, phylogeny, ecology (Matthews et al. 2018a), and predict possible host-symbiont interactions preventing impacts on conservation (Alvarez et al. 2010).

In the systems described above, it is possible to estimate the distribution of symbionts in two ways: 1 – by recovering the symbiont composition along with a host species distribution, which gives insights into the dispersal ability and the environmental requirements of a symbiont based on the host sampling; and 2 – by assessing the distribution of a singular (or a set of) symbiont species, which may differ from the host distribution depending on the symbiont host specificity. The first measure requires a broad sampling of a specific host species along with its distribution, whereas the second requires sampling all potential hosts.

Regarding feather mites, examples of a broad sampling of mites on particular hosts include the first studies evaluating their biogeography, done by Gaud & Atyeo (1976). In this study, patchy distributions of mites were recognized on introduced and widespread hosts such as the Rock Pigeon *Columba livia* Gmelin, 1789, the House Sparrow *Passer domesticus* (Linnaeus, 1758), and Domestic Chickens *Gallus gallus domesticus* (Linnaeus, 1758) (Gaud & Atyeo 1976). These ubiquitous hosts have acquired distinct, yet congeneric, mite species according to their geographic location by interacting with local and phylogenetically similar hosts (Dabert 2004; Gaud 1992; Gaud & Atyeo 1976). In these situations, feather mite species from the set of their regular mite fauna may fail to disperse along with their hosts (i.e., founder effect), leaving available microhabitats for new species to colonize, an event known as "*missing the boat*" in cophylogenetic studies (MacLeod et al. 2010). The reverse is also possible, where the arrival of a new host may change the specificity of a locally adapted symbiont, ending in a successful host shift event that may expand the original symbiont's geographic distribution (Poulin et al. 2011; Wells & Clark 2019).

Unlike introduced hosts, mite composition on naturally widespread hosts is likely affected by past evolutionary and biogeographic events rather than by recent host-to-host interactions allowed by human expansion (Dabert 2004; Hernandes et al. 2014; Klimov et al. 2017). In these cases, different host populations may present different mite compositions evidenced by the presence, absence, or replacement of either precise morphologically

established mite species, or “hidden” molecular structuration, often in the form of cryptic species (Doña et al. 2015). Barriers are usually responsible for these scenarios among host populations, preventing the mites from colonizing the totality of hosts, and creating vicariance events. An example of such a pattern is a report done by Dabert and Mironov (1999) regarding the feather mite genus *Scutulanyssus* (Pteronyssidae) on European populations of the Common House-Martin *Delichon urbicum* (Linnaeus, 1758) separated by the Ural mountains, where European and Asiatic populations of House-Martin presented distinct and morphologically well-defined species of *Scutulanysus*, indicating that the Ural mountains are a barrier for their hosts (Dabert & Mironov 1999). Other cases include different species of the mite genera *Falculifer* (Pterolichoidea: Falculiferidae) on different pigeon species around the world, where the species *F. rostratus* (Buchholz, 1869) is found in Eurasia, northern Africa, and South America, whereas *F. lacertosus* Gaud, 1976 occurs in central and southern Africa, India, and the far East (Dabert 2004; Dabert & Mironov 1999; Gaud & Atyeo 1976).

Further analysis of mite distribution on pigeons was done by Grossi and Proctor (2020) for domestic pigeons in Canada. In this study, the authors found that some of the feather mite species were patchily distributed according to humidity and temperature variables, e.g., regions with higher humidity presented a higher diversity of vane-dwelling mites compared to drier regions. Additionally, some of the mite species’ low load and low prevalence were also attributed to their inability to disperse among hosts (e.g., for down and skin dwellers feather mites), highlighting the ability to disperse as an important factor shaping their distribution. Melendéz et al. (2014) also detected irregular mite composition due to climate on passerines in Spain. Unlike Canadian pigeons, the mites in Spain presented higher infestation and prevalence in warmer and drier environments, being the temperature more relevant than precipitation for their distribution. The temperature also explained the decline in mite populations along the altitudinal elevation better than the variation in precipitation in Melendéz’s study. Effects of external temperature also influenced how feather mites were arranged on the feathers of blue tits *Cyanistes caeruleus* (Linnaeus, 1758) in the United Kingdom (Wiles et al. 2000); and is possibly one of the reasons behind the feather mite’s movements at night (Labrador et al. 2021).

The studies above indicate that the environmental conditions may affect feather mites’ biogeography, restricting their populations. Despite having a low impact when compared to biotic factors (i.e., host community), abiotic factors are also an important variable for shaping the feather mite richness globally, being the temperature more relevant than precipitation, i.e.,

warmer regions hold higher feather mite richness than temperate regions (Gusmão et al. 2020). The studies also show the importance of assessing symbiont's prevalence and abundance in host populations, as these metrics may give insights into the mite's potential to disperse. The prevalence and the mite load, on the other hand, might also vary according to a myriad of factors such as season of the year, reproductive status of the host, feather mite natural history, environmental condition, and host condition, turning the inference of the biogeography of feather mites a challenging task (Enout et al. 2012; Figureuerola 2000; Jovani & Serrano 2001; Marini et al. 1996; Matthews et al. 2018b; Thompson et al. 1997).

Despite the major macroevolutionary effect of host switch in feather mites (Doña et al. 2017b), the specificity and the host community (biotic factors) are undoubtedly essential features for feather mite disposition around the globe (Doña et al. 2018a; Gusmão et al. 2020). Examples include cophylogenetic studies, which intrinsically connect with biogeographic investigations, especially historical biogeography (Klimov et al. 2017; Matthews et al. 2018a; Štefka et al. 2011; Weckstein 2004). In feather mites, these studies differ by the taxonomic scale of the investigations, i.e., at micro- (intraspecific level) and macroevolutionary (between species, genus, and above) scales. Examples of the macroevolutionary scale include the historical biogeographic investigation of the mite genera *Proctophyllodes*, a genus presented globally on passeriform birds that shows clear patterns of geographic disposition (Klimov et al. 2017). Further macroevolutionary examples include cophylogenetic studies of the mite families Ptiloxenidae and Avenzoariidae, providing biogeographic insights into their present host-symbiont associations (Dabert et al. 2001; Dabert & Ehrnsberger 1998). On the microevolutionary side, the studies include investigating co-phylogeographic patterns of *Analges* populations on Galápagos mockingbirds (*Mimus* spp.), in the Galápagos archipelago (Štefka et al. 2011). In this study, the authors found strong accordance between bird and mite phylogenies with their distribution in the archipelago and, therefore, a high level of host co-speciation. Differently, in warblers (Parulidae) from North America, the distribution of *Amerodectes* and *Proctophyllodes* species was more related to their host ecology (i.e., nesting locations) than to host phylogeny or distribution (Matthews et al. 2018a).

Overall, data on the geographic distribution of feather mites are essential to understanding the requirements for their host specificity. However, the lack of substantial literature concerning feather mite biogeography, especially in the Neotropics, prevents any categorical inference regarding this subject.

REFERENCES

Agosta, S.J., Janz, N. & Brooks, D.R. (2010) How specialists can be generalists: Resolving the and "parasite paradox" and implications for emerging infectious disease. *Zoologia* 27, 151–162. https://doi.org/10.1590/S1984-46702010000200001

Alvarez, N., McKey, D., Kjellberg, F., & Hossaert-McKey, M. (2010) Phylogeography and historical biogeography of obligate specific mutualists. Chapter 3. In: Morand, S. & Krasnov, B.R. (ed.) *The biogeography of host-parasite interactions*, Oxford University Press, 287p.

Arribas, P., Andújar, C., Moraza, M.L., Linard, B., Emerson, B.C. & Vogler, A.P. (2020) Mitochondrial metagenomics reveals the ancient origin and phylodiversity of soil mites and provides a phylogeny of the Acari. *Molecular Biology and Evolution* 37, 683–694. https://doi.org/10.1093/molbev/msz255

Astié, A.A. & Reboreda, J.C. (2006) Costs of egg punctures and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) at Creamy-bellied Thrush (*Turdus amaurochalinus*) nests. *Auk* 123, 23–32. https://doi.org/10.1642/0004-8038(2006)123[0023:COEPAP]2.0.CO;2

Atyeo, A.W.T. & Gaud, J. (1983) Feather Mites of Obligate Brood Parasites. *The Journal of Parasitology* 69, 455–458. https://doi.org/10.2307/3281353

Atyeo, W.T. & Braasch, N.L. (1966) The feather mite genus *Proctophyllodes* (Sarcoptiformes: Proctophyllodidae). *Bulletin of the University of Nebrasca State Museum* 5, 1–354.

Azpiroz, A.B. (2015) Shiny cowbird (*Molothrus bonariensis*) parasitism records for three globally threatened species from the South American Pampas. *Wilson Journal of Ornithology* 127, 746–752. https://doi.org/10.1676/15-007

Bassini-Silva, R., Jacinavicius, F.D.C., Pereira, J.S., Werther, K., Spicer, G.S. & Barros-Battesti, D.M. (2019) Parasitism of the nasal mite *Sternostoma tracheacolum* lawrence, 1948 (Mesostigmata: Rhinonyssidae) in captive birds in Brazil. *Revista Brasileira de Parasitologia Veterinaria* 28, 754–759. https://doi.org/10.1590/s1984-29612019053

Beaulieu, F., Knee, W., Nowell, V., Schwarzfeld, M., Lindo, Z., Behan-Pelletier, V.M., Lumley, L., Young, M.R., Smith, I., Proctor, H.C., Mironov, S. V., Galloway, T.D., Walter, D.E. & Lindquist, E.E. (2019) Acari of Canada. *ZooKeys* 2019, 77–168. https://doi.org/10.3897/zookeys.819.28307

Berla, H.F. (1959) Analgesidae Neotropicais. II-Três novas espécies de *Trouessartia* Canestrini, 1889 (Acarina - Proctophyllonidae), hóspedes de Fringillidae (Aves - Passeriformes). *Boletim do Museu Nacional, New Series Zoologia* 208, 1–8.

Bernardon, F.F., Soares, T. de A.L., Vieira, T.D. & Müller, G. (2016) Helminths of *Molothrus bonariensis* (Gmelin, 1789) (Passeriformes: Icteridae) from southernmost Brazil. *Brazilian Journal of Veterinary Parasitology* 25, 279–285.

Blanco, G., Tella, J.L. & Potti, J. (1997) Feather mites on group-living Red-billed Choughs: a non-parasitic interaction? *Journal of Avian Biology* 28, 197–206.

https://doi.org/10.2307/3676970

Blanco, G., Tella, J.L., Potti, J. & Baz, A. (2001) Feather mites on birds: Costs of parasitism or conditional outcomes? *Journal of Avian Biology* 32, 271–274. https://doi.org/10.1111/j.0908-8857.2001.320310.x

Bochkov, A. V. (2011) Evolution of parasitism in mammal-associated mites of the Psoroptidia group (Acari: Astigmata). *Entomological Review* 91, 1206–1215. https://doi.org/10.1134/S0013873811090168

Bochkov, A. V., Oconnor, B.M. & Klompen, H. (2015) A review of the mite subfamily Harpirhynchinae (Acariformes: Harpirhynchidae) - Parasites of New World birds (Aves: Neognathae). *Zootaxa* 4023, 1–130. https://doi.org/10.11646/zootaxa.4023.1.1

Bochkov, A. V & Mironov, S. V. (2008) The phenomenon of phylogenetic synhospitality in acariform mites (acari: acariformes) - the permanent parasites of vertebrates. *Parazitologiia* 42, 81–100.

Bush, S.E. & Clayton, D.H. (2018) Anti-parasite behaviour of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373. https://doi.org/10.1098/rstb.2017.0196

Bush, S.E., Villa, S.M., Altuna, J.C., Johnson, K.P., Shapiro, M.D. & Clayton, D.H. (2019) Host defense triggers rapid adaptive radiation in experimentally evolving parasites. *Evolution Letters* 3, 120–128. https://doi.org/10.1002/evl3.104

Camargo-Mathias, M.I., Furquim, K.C.S., Abreu, R.M.M. de, Sodelli, L.F. & Pereira, M.C. (2020) Atualidades em Medicina Tropical no Brasil: Veterinária *Doenças Transmitidas Por Carrapatos De Importância Médica-Veterinária*. 12–51 pp.

Cavalcanti, R.B. (1988) Shiny cowbird parasitism in central Brazil. *The Condor* 90, 40–43. https://doi.org/10.2307/1368430

Černý, V. (1974) Parasitic mites of Surinam XXXI. New species of Proctophyllodidae (Sarcoptiformes, Analgoidea). *Folia Parasitologica* 21, 349–361.

Cicchino, A.C. & Castro, D.C. (1996) Revisión preliminar de las especies del género *Brueelia* Kéler, 1936 (Phthiraptera, Philopteridae) parásitas de Icterinae (Aves, Passeriformes, Fringillidae). *Graellsia* 52, 3–30.

Clayton, D.H., Bush, S.E., Goates, B.M. & Johnson, K.P. (2003) Host defense reinforces host-parasite cospeciation. *Proceedings of the National Academy of Sciences of the United States of America* 100, 15694–15699. https://doi.org/10.1073/pnas.2533751100

Clayton, D.H., Bush, S.E. & Johnson, K.P. (2015) Coevolution of Life on Hosts *Coevolution of Life on Hosts*. University of Chicago Press, 294 pp.

Crespo-Pérez, V., Pinto, C.M., Carrión, J.M., Jarrín-E, R.D., Poveda, C. & de Vries, T. (2016) The Shiny Cowbird, Molothrus bonariensis (Gmelin, 1789) (Aves: Icteridae), at 2,800 m asl in Quito, Ecuador. *Biodiversity Data Journal* 4. https://doi.org/10.3897/BDJ.4.e8184

Cruz, A., López-Ortiz, R., Ventosa-Febles, E.A., Wiley, J.W., Nakamura, T.K., Ramos-Alvarez, K.R. & Post, W. (2005) Ecology and Management of Shiny Cowbirds (*Molothrus bonariensis*) and Endangered Yellow-Shouldered Blackbirds (*Agelaius xanthomus*) in Puerto Rico. *Ornithological Monographs*, 38–44. https://doi.org/10.2307/40166813

Dabert, J. (2004) Feather mites (Astigmata; Pterolichoidea, Analgoidea) and birds as models for cophylogenetic studies. *Phytophaga* 14, 409–424.

Dabert, J., Dabert, M. & Mironov, S. V. (2001) Phylogeny of feather mite subfamily Avenzoariinae (Acari: Analgoidea: Avenzoariidae) inferred from combined analyses of molecular and morphological data. *Molecular Phylogenetics and Evolution* 20, 124–135. https://doi.org/10.1006/mpev.2001.0948

Dabert, J. & Ehrnsberger, R. (1998) Phylogeny of the feather mite family Ptiloxenidae Gaud, 1982 (Acari: Pterolichoidea). In: E. Eberman (Ed), *Arthropod Biology: Contributions to Morphology, Ecology and Systematics*. Biosystematics and Ecology Series, Vienna, pp. 145–178.

Dabert, J. & Ehrnsberger, R. (1999) Systematics of the feather mite genus *Montchadskiana* Dubinin, 1951 (Pterolichoidea, Pterolichidae, Magimeliinae) with description of five new species. *Acta zoologica cracoviensia* 42, 219–249.

Dabert, J. & Mironov, S. V (1999) Origin and evolution of feather mites. *Experimental and Applied Acarology* 23, 437–454.

Dabert, M., Coulson, S.J., Gwiazdowicz, D.J., Moe, B., Hanssen, S.A., Biersma, E.M., Pilskog, H.E. & Dabert, J. (2015) Differences in speciation progress in feather mites (Analgoidea) inhabiting the same host: the case of *Zachvatkinia* and *Alloptes* living on arctic and long-tailed skuas. *Experimental and Applied Acarology* 65, 163–179. https://doi.org/10.1007/s10493-014-9856-1

Dabert, M., Witalinski, W., Kazmierski, A., Olszanowski, Z. & Dabert, J. (2010) Molecular phylogeny of acariform mites (Acari, Arachnida): Strong conflict between phylogenetic signal and long-branch attraction artifacts. *Molecular Phylogenetics and Evolution* 56, 222–241. https://doi.org/10.1016/j.ympev.2009.12.020

Doña, J., Diaz-Real, J., Mironov, S., Bazaga, P., Serrano, D. & Jovani, R. (2015) DNA barcoding and minibarcoding as a powerful tool for feather mite studies. *Molecular Ecology Resources* 15, 1216–1225. https://doi.org/10.1111/1755-0998.12384

Doña, J., Potti, J., De La Hera, I., Blanco, G., FrÍas, O. & Jovani, R. (2017a) Vertical transmission in feather mites: insights into its adaptive value. *Ecological Entomology* 42, 492–499. https://doi.org/10.1111/een.12408

Doña, J., Proctor, H., Mironov, S., Serrano, D. & Jovani, R. (2018a) Host specificity, infrequent major host switching and the diversification of highly host-specific symbionts: The case of vane-dwelling feather mites. *Global Ecology and Biogeography* 27, 188–198. https://doi.org/10.1111/geb.12680

Doña, J., Proctor, H., Serrano, D., Johnson, K.P., Oploo, A.O. van, Huguet-Tapia, J.C., Ascunce, M.S. & Jovani, R. (2018b) Feather mites play a role in cleaning host feathers:

New insights from DNA metabarcoding and microscopy. *Molecular Ecology*. https://doi.org/10.1111/mec.14581

Doña, J., Serrano, D., Mironov, S., Montesinos-Navarro, A. & Jovani, R. (2019) Unexpected bird–feather mite associations revealed by DNA metabarcoding uncovers a dynamic ecoevolutionary scenario. *Molecular Ecology* 28, 379–390. https://doi.org/10.1111/mec.14968

Doña, J., Sweet, A.D., Johnson, K.P., Serrano, D., Mironov, S. & Jovani, R. (2017b) Cophylogenetic analyses reveal extensive host-shift speciation in a highly specialized and host-specific symbiont system. *Molecular Phylogenetics and Evolution* 115, 190–196. https://doi.org/10.1016/j.ympev.2017.08.005

Dowling, D.K., Richardson, D.S. & Komdeur, J. (2001) No effects of a feather mite on body condition, survivorship, or grooming behavior in the Seychelles warbler, *Acrocephalus sechellensis*. *Behavioral Ecology and Sociobiology* 50, 257–262. https://doi.org/10.1007/s002650100360

Dubinin, V.B. (1951) Feather mites (Analgesoidea). Part I. Introduction to study. Fauna of the USSR, Paukoobraznye. *Publisher Nauka* 6, 363 [in Russian].

Dubinin, V.B. (1953) Feather mites (Analgesoidea). Part II. Families Epidermoptidae and Freyanidae. Fauna of the USSR, Paukoobraznye. *Publisher Nauka* 6, 411 [in Russian].

Dubinin, V.B. (1956) Feather mites (Analgesoidea). Part III. Family Pterolichidae. Fauna SSSR, Paukoobraznye. *Publisher Nauka* 6, 814. [in Russian].

Enout, A.M.J., Lobato, D.N.C., Diniz, F.C. & Antonini, Y. (2012) Chewing lice (Insecta, Phthiraptera) and feather mites (Acari, Astigmata) associated with birds of the Cerrado in Central Brazil. *Parasitology Research* 111, 1731–1742. https://doi.org/10.1007/s00436-012-3016-5

Faccini, J.L.H., Gaud, J. & Atyeo, W.T. (1976) Descrição de *Eurydiscalges* g.n. (Analgidae, Sarcoptiformes), com quatro espécies novas parasitas de Psittacidae (Aves) provenientes da América do Sul. *Revista Brasileira De Biologia* 36, 701–707.

Fain, A. (1965) A review of the family Epidermoptidae Trouessart parasitic on the skin of birds (Acarina: Sarcoptiformes). *Verhandelingen van de Koninklijke vlaamse academie voor wetenschappen, letteren en schone kunsten van België, Klasse der wetenschapen* 84, 1-176 (I);-1-144 (II).

Fain, A., Bochkov, A. V. & Corpuz-Raros, L.A. (2002) 72 Bulletin de l'Institut royal des Sciences Naturelles de Belgique *A revision of the Hemicheyletia generic group (Acari: Cheyletidae)*. 27–66 pp.

Faleiro, D.C.C., Toldi, M., Da Silva, G.L. & Ferla, N.J. (2015) The ectoparasites *Dermanyssus gallinae* and *Megninia ginglymura*: Bioecology and natural enemies in commercial egg-laying hens. *Systematic and Applied Acarology* 20, 861–874. https://doi.org/10.11158/saa.20.8.3

Figureuerola, J. (2000) Ecological correlates of feather mite prevalence in passerines. *Journal of Avian Biology* 31, 489–494.

Fiorini, V.D., De Mársico, M.C., Ursino, C.A. & Reboreda, J.C. (2019) Obligate Brood Parasitism on Neotropical Birds. In: *Behavioral Ecology of Neotropical Birds*. Springer International Publishing, Cham, pp. 103–131.

Galván, I., Aguilera, E., Atiénzar, F., Barba, E., Blanco, G., Cantó, J.L., Cortés, V., Frías, Ó., Kovács, I., Meléndez, L., Møller, A.P., Monrós, J.S., Pap, P.L., Piculo, R., Senar, J.C., Serrano, D., Tella, J.L., Vágási, C.I., Vögeli, M. & Jovani, R. (2012) Feather mites (Acari: Astigmata) and body condition of their avian hosts: A large correlative study. *Journal of Avian Biology* 43, 273–279. https://doi.org/10.1111/j.1600-048X.2012.05686.x

Gaud, J. (1992) Acquisition d'hotes nouveaux par les Acariens plumicoles. *Bulletin de la Société Française de Parasitologie* 10, 79–91.

Gaud, J. & Atyeo, W.T. (1976) Discordance entre les aires de répartition géographique des parasites et celles de leur hôtes chez les Sarcoptiformes plumicoles. *Acarologia* 18, 329–344.

Gaud, J. & Atyeo, W.T. (1977) Nouvelles superfamilles pour les Acariens astigmates parasites d'oiseaux. *Acarologia* 19, 678–685.

Gaud, J. & Atyeo, W.T. (1996) Feather mites of the world (Acarina, Astigmata): The supraspecific Taxa. *Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques* 277 (Pt.1, 1-193 (text) & 1-436 (illustrations).

González-Acuña, D., Vergara, F., Moreno, L., Barrientos, C., Ardiles, K. & Cicchino, A. (2006) Lice (Insecta: Phthiraptera) from species of the families Furnariidae, Tyrannidae, Turdidae and icteridae (Aves: Passeriformes) from Chile. *Gayana* 70, 210–219. https://doi.org/10.4067/S0717-65382006000200008

Gusmão, R.A.F., Hernandes, F.A., Vancine, M.H., Naka, L.N. & Doña, J. (2020) Host diversity outperforms climate as a global driver of symbiont diversity in the bird-feather mite system. *Diversity and Distributions* 27, 416–426. https://doi.org/10.1111/ddi.13201

Hernandes, F.A. (2021) New records of feather mites (Sarcoptiformes: Proctophyllodidae) on tanagers (Passeriformes: Thraupidae) from Brazil. *Entomological Communications* 3, 1–4. https://doi.org/10.37486/2675-1305.ec03039

Hernandes, F.A., Pedroso, L.G.A. & Mironov, S. V. (2014) From cuckoos to chickens: a caught-in-the-act case of host shift in feather mites (Arachnida: Acari: Psoroptoididae). *Parasitology Research* 113, 4355–4361. https://doi.org/10.1007/s00436-014-4110-7

Hernandes, F.A., Valim, M.P. & Mironov, S. V. (2010) On the identity of Pterodectes ralliculae Atyeo and Gaud, 1977 (Astigmata: Proctophyllodidae). *Journal of Natural History* 44, 369–377. https://doi.org/10.1080/00222930903383594

Hilario-Pérez, A.D. & Dowling, A.P.G. (2020) Prevalence and new host records of nasal mites (Acari: Rhinonyssidae: Ereynetidae: Turbinoptidae) in birds from Arkansas and Illinois (United States). *International Journal of Acarology* 46, 589–594. https://doi.org/10.1080/01647954.2020.1837949

Horn, T.B., Granich, J., Körbes, J.H., Da Silva, G.L. & Ferla, N.J. (2018) Mite fauna (Acari)

associated with the poultry industry in different laying hen management systems in Southern Brazil: A species key. *Acarologia* 58, 140–158. https://doi.org/10.24349/acarologia/20184233

Jacinavicius, F. de C., Bassini-Silva, R., Mendoza-Roldan, J.A., Pepato, A.R., Ochoa, R., Welbourn, C. & Barros-Battesti, D.M. (2018) A checklist of chiggers from Brazil, including new records (Acari: Trombidiformes: Trombiculidae and leeuwenhoekiidae). *ZooKeys* 2018, 1–41. https://doi.org/10.3897/zookeys.743.22675

Johnson, K.P., Weckstein, J.D., Witt, C.C., Faucett, R.C. & Moyle, R.G. (2002) The perils of using host relationships in parasite taxonomy: Phylogeny of the *Degeeriella* complex. *Molecular Phylogenetics and Evolution* 23, 150–157. https://doi.org/10.1016/S1055-7903(02)00014-3

Jovani, R. & Serrano, D. (2001) Feather mites (Astigmata) avoid moulting wing feathers of passerine birds. *Animal Behaviour* 62, 723–727. https://doi.org/10.1006/anbe.2001.1814

Klimov, P.B., Mironov, S. V. & OConnor, B.M. (2017) Detecting ancient codispersals and host shifts by double dating of host and parasite phylogenies: Application in proctophyllodid feather mites associated with passerine birds. *Evolution* 71, 2381–2397. https://doi.org/10.1111/evo.13309

Klimov, P.B. & Oconnor, B.M. (2013) Is permanent parasitism reversible? - Critical evidence from early evolution of house dust mites. *Systematic Biology* 62, 411–423. https://doi.org/10.1093/sysbio/syt008

Knee, W., Proctor, H. & Galloway, T. (2008) Survey of nasal mites (Rhinonyssidae, Ereynetidae, and Turbinoptidae) associated with birds in Alberta and Manitoba, Canada. *Canadian Entomologist* 140, 364–379. https://doi.org/10.4039/n08-017

Knowles, L.L. & Klimov, P.B. (2011) Estimating phylogenetic relationships despite discordant gene trees across loci: The species tree of a diverse species group of feather mites (Acari: Proctophyllodidae). *Parasitology* 138, 1750–1759. https://doi.org/10.1017/S003118201100031X

Krantz, G.W. & Walter, D.E. (2009) *A Manual of Acarology (3rd edition)*. 3rd ed. Texas University Press, Lubbock, 807 pp.

Labrador, M.D.M., Doña, J., Serrano, D. & Jovani, R. (2021) Feather mites at night: an exploration of their feeding, reproduction, and spatial ecology. *The Scientific Naturalist* 103, 1–5. https://doi.org/10.1002/ecy.3550

Levy, C. (2019) Records of the Shiny Cowbird (*Molothrus bonariensis*) in Jamaica. *The Journal of Caribbean Ornithology* 32, 86–90.

Lindholm, A.K., Venter, G.J. & Ueckermann, E.A. (1998) Persistence of passerine ectoparasites on the diederik cuckoo *Chrysococcyx caprius*. *Journal of Zoology* 244, 145–153. https://doi.org/10.1017/S0952836998001162

Longdon, B., Hadfield, J.D., Day, J.P., Smith, S.C.L., McGonigle, J.E., Cogni, R., Cao, C. & Jiggins, F.M. (2015) The Causes and Consequences of Changes in Virulence following Pathogen Host Shifts. *PLoS Pathogens* 11, 1–18.

https://doi.org/10.1371/journal.ppat.1004728

Lowther, P.E. (2019) Lists of victims and hosts of the parasitic cowbirds (*Molothrus*). *Field Museum of Natural History, Chicago, Illinois, USA*. Available from: https://www.fieldmuseum.org/blog/brood-parasitism-host-lists (August 26, 2020)

Lozano-Fernandez, J., Tanner, A.R., Giacomelli, M., Carton, R., Vinther, J., Edgecombe, G.D. & Pisani, D. (2019) Increasing species sampling in chelicerate genomic-scale datasets provides support for monophyly of Acari and Arachnida. *Nature Communications* 10. https://doi.org/10.1038/s41467-019-10244-7

MacLeod, C.J., Paterson, A.M., Tompkins, D.M. & Duncan, R.P. (2010) Parasites lost - do invaders miss the boat or drown on arrival? *Ecology Letters* 13, 516–527. https://doi.org/10.1111/j.1461-0248.2010.01446.x

Marín, M. (2000) The Shiny Cowbird (*Molothrus bonariensis*) in Chile: Introduction or Dispersion? Its Hosts and Parasitic Trends. *Ornitologia Neotropical* 11, 285–296.

Marini, M., Reinert, B., Bornschein, M., Pinto, J. & Pichorim, M. (1996) Ecological correlates of ectoparasitism on Atlantic Forest birds, Brazil. *Ararajuba* 4, 93–102.

Matthews, A.E., Klimov, P.B., Proctor, H.C., Dowling, A.P.G., Diener, L., Hager, S.B., Larkin, J.L., Raybuck, D.W., Fiss, C.J., McNeil, D.J. & Boves, T.J. (2018a) Cophylogenetic assessment of New World warblers (Parulidae) and their symbiotic feather mites (Proctophyllodidae). *Journal of Avian Biology* 49, 1–17. https://doi.org/10.1111/jav.01580

Matthews, A.E., Larkin, J.L., Raybuck, D.W., Slevin, M.C., Stoleson, S.H. & Boves, T.J. (2018b) Feather mite abundance varies but symbiotic nature of mite-host relationship does not differ between two ecologically dissimilar warblers. *Ecology and Evolution* 8, 1227–1238. https://doi.org/10.1002/ece3.3738

Mena, M., Valdebenito, J.O., Moreno, L., Fuentes-Castillo, D., Kinsella, J.M., Mironov, S., Barrientos, C., Cicchino, A. & González-Acuña, D. (2020) Parasites of the Shiny Cowbird, *Molothrus bonariensis*, and the Austral Blackbird, *Curaeus curaeus*, (Passeriformes: Icteridae) in Chile. *Brazilian journal of veterinary parasitology* 29, 1–10. https://doi.org/10.1590/S1984-29612020022

Mironov, S. V. (2003) On some problems in the systematics of feather mites. *Acarina* 11, 3–29.

Mironov, S. V. (2013) *Allopsoroptoides galli* n. g., n. sp., a new genus and species of feather mites (Acari: Analgoidea: Psoroptoididae) causing mange in commercially raised domestic chicken in Brazil. *Systematic Parasitology* 85, 201–212. https://doi.org/10.1007/s11230-013-9422-y

Mironov, S. V. & Galloway, T.D. (2002) Four new species of feather mites (Acari: Analgoidea). *The Canadian Entomologist* 134, 605–618.

Mironov, S. V., Klimov, P.B., Block, N.L. & Oconnor, B.M. (2020) Feather mites of the new genus *Bernierinyssus* gen. n. (Acariformes: Pteronyssidae) from endemic Malagasy warblers (Passeriformes: Bernieridae)- A lineage showing symbiotic cospeciation with

their avian hosts. *Systematic and Applied Acarology* 25, 1765–1802. https://doi.org/10.11158/saa.25.10.5

Mironov, S. V., Literak, I. & Čapek, M. (2008) New feather mites of the subfamily Pterodectinae (Acari: Astigmata: Proctophyllodidae) from passerines (Aves: Passeriformes) in Mato Grosso do Sul, Brazil. *Zootaxa* 38, 1–38.

Mironov, S. V (1987) Morphological adaptations of feather mites superfamily Analgoidea to different types of plumage and to skin of birds. *Parasitologicheskij sbornik* 34, 114–132.

Mironov, S.V. & Malyshev, L.L. (2002) Dynamics of Infection the Chaffinch nestlings *Fringilla coelebs* with feather mites (Acari: Analgoidea). *Parazitologiia* 36, 356-374. [In Russian with English summary].

Moreno-Rueda, G. (2017) Preen oil and bird fitness: a critical review of the evidence. *Biological Reviews* 92. https://doi.org/https://doi.org/10.1111/brv.12324

Mullen, G.R. & OConnor, B.M. (2019) Mites (Acari). In: *Medical and Veterinary Entomology*. Elsevier Inc., pp. 533–602.

OConnor, B.M. (1982) Acari: Astigmata. In: S. P. Parker (Ed), *Synopsis and classification of living organisms*. McGraw-Hill, New York, pp. 146–169.

Ogrzewalska, M. & Pinter, A. (2016) Ticks (Acari: Ixodidae) as ectoparasites of Brazilian wild birds and their association with rickettsial diseases. *Brazilian Journal of Veterinary Research and Animal Science* 53, 1–31. https://doi.org/10.11606/issn.1678-4456.v53i1p1-31

Oppel, S., Schaefer, H.M., Schmidt, V. & Schröder, B. (2004) Cowbird parasitism of Pale-headed Brush-finch *Atlapetes pallidiceps*: Implications for conservation and management. *Bird Conservation International* 14, 63–75. https://doi.org/10.1017/S0959270904000103

Ortega, C.R., Cruz, A. & Mermoz, M.E. (2005) Issues and Controversies of Cowbird (*Molothrus* spp.) management. *Ornithological Monographs*, 6–15.

Ottenburghs, J. (2019) Multispecies hybridization in birds. *Avian Research* 10, 1–11. https://doi.org/10.1186/s40657-019-0159-4

Pepato, A.R. & Klimov, P.B. (2015) Origin and higher-level diversification of acariform mites - Evidence from nuclear ribosomal genes, extensive taxon sampling, and secondary structure alignment. *BMC Evolutionary Biology* 15, 1–20. https://doi.org/10.1186/s12862-015-0458-2

Philips, J.R. (2000) A review and checklist of the parasitic mites (Acarina) of the Falconiformes and Strigiformes. *Journal of Raptor Research* 34, 210–231.

Philips, J.R. & Fain, A. (1991) Acarine symbionts of louseflies (Diptera, Hippoboscidae). *Acarologia* 32, 377–384.

Post, W., Cruz, A. & McNair, D.B. (1993) The North American Invasion Pattern of the Shiny Cowbird. *Journal of Field Ornithology* 64, 32–41.

Poulin, R., Krasnov, B.R. & Mouillot, D. (2011) Host specificity in phylogenetic and geographic space. *Trends in Parasitology* 27, 355–361. https://doi.org/10.1016/j.pt.2011.05.003

Proctor, H.C. & Jones, D.N. (2004) Geographical structuring of feather mite assemblages from the Australian Brush-Turkey (Aves: Megapodiidae). *Journal of Parasitology* 90, 60–66. https://doi.org/10.1645/GE-57R

Ròzsa, L. (1993) Speciation patterns of ectoparasites and "straggling" lice. *International Journal for Parasitology* 23, 859–864. https://doi.org/10.1016/0020-7519(93)90050-9

Samplonius, J.M. & Both, C. (2014) A case of a three species mixed brood after two interspecific nest takeovers. *Ardea* 102, 105–107. https://doi.org/10.5253/078.102.0113

Sharma, P.P., Kaluziak, S.T., Pérez-Porro, A.R., González, V.L., Hormiga, G., Wheeler, W.C. & Giribet, G. (2014) Phylogenomic interrogation of arachnida reveals systemic conflicts in phylogenetic signal. *Molecular Biology and Evolution* 31, 2963–2984. https://doi.org/10.1093/molbev/msu235

Sick, H. (1997) *Ornitologia Brasileira*. 2nd ed. Nova Fronteira, Rio de Janeiro, 912 pp.

Skoracki, M., Glowska, E. & Bochkov, A. V. (2013) Phylogeny of quill mites of the family Syringophilidae (Acari: Prostigmata) based on their external morphology. *European Journal of Entomology* 110, 663–675. https://doi.org/10.14411/eje.2013.090

Smith, J.N.M., Taitt, M.J. & Zanette, L. (2002) Removing brown-headed cowbirds increases seasonal fecundity and population growth in song sparrows. *Ecology* 83, 3037–3047. https://doi.org/10.1890/0012-9658(2002)083[3037:RBHCIS]2.0.CO;2

Soares, N.M., Tucci, E.C., Freitas, E.R. & Fernandes, D.P.B. (2016) Reduced productivity among confined laying hens infested by *Allopsoroptoides galli* (Mironov, 2013). *Poultry Science* 95, 819–822. https://doi.org/10.3382/ps/pev442

Soler, M. (2017) *Avian Brood Parasitism: Behavioral, Ecology, Evolution and Coevolution*. M. Soler (Ed). Springer International Publishing, 574 pp.

Sorenson, M.D., Balakrishnan, C.N. & Payne, R.B. (2004) Clade-limited colonization in brood parasitic finches (*Vidua* spp.). *Systematic Biology* 53, 140–153. https://doi.org/10.1080/10635150490265021

Štefka, J., Hoeck, P.E., Keller, L.F. & Smith, V.S. (2011) A hitchhikers guide to the Galápagos: Co-phylogeography of Galápagos mockingbirds and their parasites. *BMC Evolutionary Biology* 11. https://doi.org/10.1186/1471-2148-11-284

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

Sykes Jr, P.W. & Post, W. (2001) First specimen and Evidence of Breeding by the Shiny Cowbird in Georgia. *The Oriole* 66, 45–51.

Thompson, C.W., Hillgarth, N., Leu, M. & Mcclure, H.E. (1997) High Parasite Load in House Finches (*Carpodacus mexicanus*) is correlated with reduced expression of a

sexually selected trait. *The American Midland Naturalist* 149, 270–294.

Tompkins, D.M. & Clayton, D.H. (1999) Host resources govern the specificity of swiftlet lice: Size matters. *Journal of Animal Ecology* 68, 489–500. https://doi.org/10.1046/j.1365-2656.1999.00297.x

Tucci, E.C., Rebouças, M.M., Mendes, M.C. & Gama, N.M.S.Q. (2005) Infestação por *Megninia* spp. em criação industrial de aves produtoras de ovos para consumo. *Arquivos do Instituto Biológico* 72, 121–124.

Tucci, E.C., Soares, N.M., Faccini, J.L.H. & Boas, D.V. (2014) Additional information about a mange outbreak by *Allopsoroptoides galli* (Acari: Psoroptoididae) in commercial laying hens in the state of São Paulo, Brazil. *Pesquisa Veterinaria Brasileira* 34, 760–762. https://doi.org/10.1590/S0100-736X2014000800009

Tuero, D.T., Fiorini, V.D. & Reboreda, J.C. (2007) Effects of Shiny Cowbird *Molothrus bonariensis* parasitism on different components of House Wren *Troglodytes aedon* reproductive success. *Ibis* 149, 521–529. https://doi.org/10.1111/j.1474-919X.2007.00676.x

Valim, M.P. & Hernandes, F.A. (2008) Redescriptions of five species of the feather mite genus *Pterodectes* Robin, 1877 (Acari: Proctophyllodidae: Pterodectinae), with the proposal of a new genus and a new species. *Acarina* 16, 131–157.

Valim, M.P., Hernandes, F.A. & Proctor, H.C. (2011) Feather mites of Brazil (Acari: Astigmata: Analgoidea and Pterolichoidea). *International Journal of Acarology* 37, 293–324. https://doi.org/10.1080/01647954.2010.519719

Vas, Z., Fuisz, T.I., Fehérvári, P., Reiczigel, J. & Rozsa, L. (2013) Avian brood parasitism and ectoparasite richness-scale-dependent diversity interactions in a three-level host-parasite system. *Evolution* 67, 959–968. https://doi.org/doi:10.1111/j.1558-5646.2012.01837.x

Walter, D.E. & Proctor, H.C. (2013) *Mites: Ecology, Evolution & Behaviour*. Springer Netherlands, Dordrecht. Available from: https://link.springer.com/book/10.1007/978-94-007-7164-2

Weckstein, J.D. (2004) Biogeography explains cophylogenetic patterns in toucan chewing lice. *Systematic Biology* 53, 154–164. https://doi.org/10.1080/10635150490265085

Wells, K. & Clark, N.J. (2019) Host Specificity in Variable Environments. *Trends in Parasitology* 35, 452–465. https://doi.org/10.1016/j.pt.2019.04.001

Wiles, R., Cameron, J., Behnke, J.M., Hartley, I.R., Gilbert, F.S. & McGregor, P.K. (2000) Wing feather mite infestations on passerine birds: season and ambient air temperature influence the distribution of *Proctophyllodes stylifer* across the wings of blue tits (*Parus caeruleus*). *Canadian Journal of Zoology* 78, 1397–1407. https://doi.org/10.1139/cjz-78-8-1397

Zohdy, S., Kemp, A.D., Durden, L.A., Wright, P.C. & Jernvall, J. (2012) Mapping the social network: tracking lice in a wild primate (*Microcebus rufus*) population to infer social contacts and vector potential. *BMC Ecology* 12, 11. https://doi.org/10.1186/1472-6785-