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Extensive *in situ* radiation of feather lice on tinamous

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Tinamous host the highest generic diversity of lice of any group of birds, as well as hosting representatives of all four avian feather louse ecomorphs. Although the generic diversity of tinamou feather lice is well documented, few attempts have been made to reconstruct the phylogenetic relationships among these lice. To test whether tinamou feather lice form a monophyletic group as a whole, we used whole-genome sequencing to estimate a higher-level phylogeny of tinamou feather lice, together with a broad diversity of other avian feather louse groups. In total, we analysed sequences from over 1000 genes for 48 genera of avian lice using both concatenated and coalescent approaches to estimate the phylogeny of this diverse group of avian feather lice. Although the body louse ecomorph of tinamou feather lice formed a monophyletic group, they did not strictly form a monophyletic group together with the other three ecomorphs of tinamou feather lice. In particular, a clade comprised of several feather louse genera, mainly from South America, is nested phylogenetically within tinamou lice, which also have their main centre of diversity in South America. These results suggest *in situ* radiation of these parasites in South America.

1. Introduction

Parasites make up a large portion of life on earth [1,2]. However, this diversity is not evenly distributed across biogeographic regions nor across host lineages. Just as in free-living organisms, diversity of most parasites is higher in the tropics [3,4]. In this case, parasite diversity may be directly tied to host diversity [5], because parasites depend on their hosts for survival and reproduction. Diversity of parasites also varies across different host lineages [6]. While aspects of host biology and host ecology likely play important roles in dictating this variation [6], it is also important to understand the evolutionary processes and patterns generating this diversity.

One group of parasites in which diversity varies substantially across different groups of hosts are feather lice (Phthiraptera: Ischnocera: Philopteridae), with some host species harbouring a single genus and others harbouring up to 10 genera [7]. These insects are permanent ectoparasites of birds and complete their entire life cycle on the host [7], where they feed primarily on the downy portions of host feathers [8]. This group of lice is generally incapable of locomotion off of feathers, and is so specialized to life in the feathers, that they will stay on the host body even when the host dies [8].

Avian feather lice have also diverged into multiple 'ecomorphs,' which are characterized by drastic differences in morphology that have evolved to escape host preening defences [9,10]. Feather lice of the 'wing' ecomorph have a long and slender body form, and escape from host preening by inserting between the barbs of the wing feathers [11]. Feather lice of the 'body' ecomorph, by

contrast, have a rounded body form with rounded head margin and escape from host preening by burrowing into their host's body feathers [12]. Feather lice of the 'head' ecomorph have a rounded body form with a triangular head margin and live on the head to escape host preening in a region of the host's body that the bird cannot reach with its bill. However, head lice must resist scratching, the principle method that birds use to preen their head. To do so, head lice grip tightly with their mandibles to the barbs of feathers on the host's head [13]. Some groups of feather lice have an intermediate body form, and this ecomorph has been termed 'generalist', because they can be found over many host body regions and likely escape host preening by running through the feathers [9,10].

Most avian lineages harbour one to three feather louse ecomorphs, but a single tinamou species can harbour all four ecomorphs (wing, body, head, and generalist). Furthermore, the diversity of louse species on a single tinamou species, or even individual tinamou host, is remarkable, with sometimes more than 10 species or genera are found on an individual bird. Thus, the evolutionary pattern of this remarkable diversity of parasites on tinamous is of considerable interest [9]. Tinamous are ground-dwelling partridge-like birds endemic to the Neotropics from Mexico to Patagonia [14], are the only living lineage of flighted palaeognaths (which also includes ostriches, rheas, emus, and kiwis), and are the most diverse order of palaeognaths with nine genera and 47 species [14]. Phylogenetically, tinamous are embedded within the ratites and are one of the oldest extant avian lineages [15–17].

Although there has been considerable work on the taxonomy and morphology of tinamou lice [9,13,18–26], there has been very little focus on their phylogenetic relationships (but see [27] for a morphological study). The majority of tinamou lice are feather lice in the chewing louse suborder Ischnocera, which is the focus of this study. Tinamous host single feather louse genera of wing, head, and generalist ecomorphs and 15 genera of the body ecomorph. In several cases, a single tinamou species can host up to eight genera of body lice, in addition to a single genera from the other three ecomorphs [7]. Based on distinct morphological features, tinamou feather lice of the body louse ecomorph, currently recognized as members of the louse family Philopteridae (Ischnocera), have often been placed into a separate family, Heptapsogasteridae [20,27,28]. A morphological phylogenetic study focused on Heptapsogasteridae assumed this clade was 'basal' in Ischnocera [27] following the concept that it is a family separate from Philopteridae within the suborder Ischnocera. However, a broader morphological study of Ischnocera [29] and subsequent molecular datasets [10,29,30] suggested that Heptapsogasteridae might be considerably more derived among avian feather lice. Furthermore, the monophyly of Heptapsogasteridae has never been tested using a molecular dataset with sufficient taxon sampling.

The phylogenetic placement of the wing (*Pseudolipeurus*), head (*Pseudophilopterus*), and generalist (*Tinamotaecola*) ecomorphs of tinamou feather lice, which are all currently placed in Philopteridae and have never been suggested to be related to Heptapsogasteridae based on morphology, is also not well understood. These genera were not included in the morphological phylogenetic study of Smith [29]. Furthermore, no molecular study has included samples of all of these genera along with the Heptapsogasteridae. However, Johnson *et al*. [10,31] included two or three tinamou louse representatives and found a sister relationship between tinamou wing (*Pseudolipeurus*) and head (*Pseudophilopterus*) lice, but their sampling of Heptapsogasteridae was poor and this family was not recovered as monophyletic. Furthermore, no phylogenetic study has included a sample of the generalist ecomorph, *Tinamotaecola*. Johnson *et al*. [32] analysed a phylogenomic dataset that included two samples of tinamou body lice (Heptapsogasteridae) and recovered these lice in a relatively derived position within avian feather lice, similar to the results of the previous studies based only on a few genes.

Given the major limitations of these prior studies, we wanted to investigate whether the myriad of feather louse genera parasitizing tinamous evolved via a single diversification event, in which tinamou lice form a monophyletic group, or multiple independent diversification events, in which tinamou lice form distinct, distantly related lineages within avian feather lice. Thus, to reconstruct the higher-level phylogeny of tinamou lice, we sequenced the genomes of single representatives of 12 different genera of tinamou lice and 32 additional louse samples of 28 additional genera, for a total of 44 samples. We targeted greater than 1100 genes and conducted phylogenomic analyses of these gene sequences using both concatenated and coalescent approaches.

2. Methods

(a) Taxon sampling and genome sequencing

For this study, we sequenced samples of all four of the tinamou louse ecomorphs (electronic supplementary material, table S1) including the single generic representatives of wing (*Pseudolipeurus*), head (*Pseudophilopterus*), and generalist (*Tinamotaecola*) tinamou louse ecomorphs, and nine genera of tinamou body lice (Heptapsogasteridae). Based on previous studies [10,32], lice from other genera and host groups were sequenced to include all genera with previously documented close phylogenetic affinities with tinamou lice, as well as a diversity of other avian feather louse genera known to be closely related to these groups (electronic supplementary material, table S1). We used a representative of the genus *Chelopistes* as the outgroup to root the tree. Genomes for 11 samples were already available from Johnson *et al*. [32] and we combined these data with data from 33 newly sequenced genomes for this study (electronic supplementary material, table S1).

Louse samples were collected from their hosts in the field using ethyl acetate fumigation or pyrethrin powder dusting methods [33]. The lice were immediately placed in 95% ethanol and were later stored at −80°C. Prior to DNA extraction, each specimen was photographed as a voucher. Whole lice were ground up individually in 1.5 ml tubes and genomic DNA was isolated using standard protocols and reagents from the Qiagen QIAamp DNA Micro Kit (Qiagen, Valencia, CA, USA). The standard protocol was modified by (i) incubating the specimens in buffer ATL (for tissue lysis) and proteinase *K* at 55°C for 48 h rather than the recommended 1–3 h and (ii) substituting buffer AE with buffer EB (elution buffer) to ensure maximal yield (greater than 5 ng) of DNA from the louse tissue. Following DNA extractions, we quantified each extraction with a Qubit 2.0 Fluorometer (Invitrogen, Carlsbad, CA, USA) using the manufacturer's recommended protocols and reagents.

Libraries were prepared from these extracts with Hyper Library construction kits (Kapa Biosystems) and sequenced with 100–160 bp paired-end reads on an Illumina HiSeq2000, 2500, or 4000. Fastq files from sequence data were generated and demultiplexed with bcl2fastq v. 2.17.1.14. All library preparation, sequencing, and fastq file generation was carried out at the W.M. Keck Center (University of Illinois, Urbana, IL, USA).

Raw reads were subsequently deposited in the National Center for Biotechnology Information (NCBI) GenBank SRA database (electronic supplementary material, table S1).

(b) Phylogenomic analyses

To obtain gene sequence data from raw genome sequencing reads for phylogenetic analysis, we used automated Target Restricted Assembly Method (aTRAM) v. 1.0 [34], which is a method that uses short read datasets to target and assemble genes across divergent taxonomic datasets [34]. Before assembly, quality metrics for each dataset were assessed using FastQC v. 0.10.1 (Babraham Bioinformatics) to screen for significant irregularities. Duplicate reads were removed using fastqSplitDups.py script in the mcscript DNA processing repository on Github (https://github.com/McIntyre-Lab/mcscript). Adaptors were identified and trimmed using fastx_clipper and all sequence reads were quality trimmed from the 3′ end to remove bases with a Phred score less than 28 using fastq_quality_trimmer – (FASTX Toolkit v. 0.0.14).

Quality trimmed fastq files were converted to aTRAM blast libraries. We then targeted 1107 single-copy 1 : 1 orthologue genes [35,36] for assembly, using *tblastn* searches of amino acid gene sequences from *Pediculus humanus* [37] with three aTRAM iterations. The resulting best contigs were processed and compiled into final gene sequences using an Exonerate v. 2.2.0 [38] pipeline to identify exon/intron boundaries, along with custom scripts to stitch together the exon regions of each locus assembled in aTRAM [36].

We aligned sequence-based nucleotides for each gene separately using PASTA v. 1.8.2 [39]. Using a custom Python script, we removed genes that contained less than five of the ingroup taxa and one outgroup taxon. We then masked sites containing greater than 40% gaps using trimAL v. 1.4 [40]. With the aligned data, we performed both concatenated and coalescent gene tree-species tree estimation methods. The aligned data matrices are deposited in Dryad. For the concatenated method, we first combined all the gene files into a single matrix using Sequence Matrix [41]. We took the data matrix and calculated guanine-cytosine (GC) content by species per codon using a custom Perl script. We performed an initial unpartitioned analysis in RAxML v. 8.1.3 [42], using a GTR + GAMMA model and 100 rapid bootstrap replicates. Bootstrap support was then summarized on a best tree. We also completed a partitioned concatenated DNA analysis using PartitionFinder v. 2.1.1 [43] to evaluate the best partitioning scheme under the corrected Akaike information criterion (AICc) [44]. RAxML was once again used to estimate the best likelihood tree from the partitioned concatenated alignment, using a GTR + GAMMA model for each partition and 100 rapid bootstrap replicates, which were then summarized on a best tree file. We completed an additional maximum-likelihood analysis using IQ-Tree v. 1.6.5 [45] using a mixed model analysis and 100 bootstrap replicates. We also ran a maximum-likelihood analysis, in which we accounted for codon degeneracy by recoding relevant bases with International Union of Pure and Applied Chemistry (IUPAC) ambiguity codes using Dengen v. 1.4 [46] to account for potential variation in GC base composition. For this analysis, we used a GTR + GAMMA model on the unpartitioned data matrix and 100 rapid bootstrap replicates in RAxML. For the coalescent analysis, we estimated gene trees for each gene alignment separately, also conducting 100 rapid bootstrap replicates in RAxML using a GTR + GAMMA model for each gene. The gene trees were summarized using ASTRAL v. 4.10.6 [47] with quartet-based [48] local posterior probability support for branches.

3. Results

After data filtering, the final dataset included sequences of 1068 genes from 44 genera of avian lice, including 12 from tinamous. The concatenated data matrix consisted of 1.6 million aligned base positions. The GC content across species and codons ranged from 0.379 to 0.456. The mean and median values for each codon were 0.422 and 0.424 for the first codon, 0.426 and 0.427 for the second codon, and 0.412 and 0.412 for the third codon position. From this data matrix, the unpartitioned concatenated maximum-likelihood analysis in RAxML produced a completely resolved and well-supported tree, with 37 of 41 nodes (greater than 90%) receiving 100% bootstrap support (figure 1). Our partitioned analysis produced a tree (electronic supplementary material, figure S1) with nearly identical topology to the non-partitioned concatenated analysis tree, and with similar support values. The ASTRAL tree was also very highly supported with 35 of 41 ingroup nodes supported by a local posterior probability of 1.0 (electronic supplementary material, figure S2). Overall, the coalescent tree produced using ASTRAL, from individual gene trees, is very similar in topology to the maximum-likelihood tree, with only two branch rearrangements: one among species of *Rallicola* and another at the base of the *Philopterus*-complex (the clade containing *Cuculoecus* through *Ardeiphagus*), both of which were supported by less than 1.0 local posterior probability. The maximum-likelihood analysis in IQ-Tree recovered GTR + F+I + G4 (general time reversible model with unequal rates and unequal base frequency, empirical base frequencies, allowing for a proportion of invariable sites plus a discrete gamma model) as the best-fit model for our dataset, and the final consensus tree was identical in topology to our unpartitioned and partitioned analysis in RAxML. Bootstrap support was also very similar between these two trees (electronic supplementary material, figure S3). After degeneracy recoding, the tree produced was strongly supported with 37 of 41 nodes receiving 100% bootstrap support and was identical in topology to the unpartitioned analysis, except for one branch rearrangement in the *Rallicola* clade (electronic supplementary material, figure S4).

All tinamou body louse genera that we sampled were recovered together in a single monophyletic clade. The lice that make up this clade are representatives of the group previously described as Heptapsogasteridae. Until recently [10], the non-body ecomorphs of tinamou lice were considered distantly related to other tinamou lice [27,29]. However, we recovered the genera *Pseudolipeurus* (wing) as sister to *Pseudophilopterus* (head) and together these were sister to *Tinamotaecola* (generalist). These three tinamou louse genera were recovered as sister to lice from non-tinamou avian hosts; however, together with tinamou body lice, these lineages comprised a larger monophyletic group primarily distributed in South America. In particular, the genera *Osculotes* and *Pessoaiella* (both parasitizing hoatzin, *Opisthocomus hoatzin*) and *Palmaellus* and *Psophiicola* (both parasitizing trumpeters, *Psophia* spp.) have exclusively South American distributions. Several of the species of *Rallicola* that we included also have hosts with distributions in South America, including woodcreepers (Dendrocolaptidae), some rails (Rallidae), some jacanas (Jacanidae), and a few *Rallicola* associated with woodpeckers (Picidae) (figure 1). Thus, tinamou lice as a whole are paraphyletic, although they only fall into two distinct, albeit closely related, groups (figure 1).

We also tested the phylogenetic placement of a group of body louse genera (sometimes termed the louse family 'Goniodidae') from landfowl (Galliformes) and pigeons and

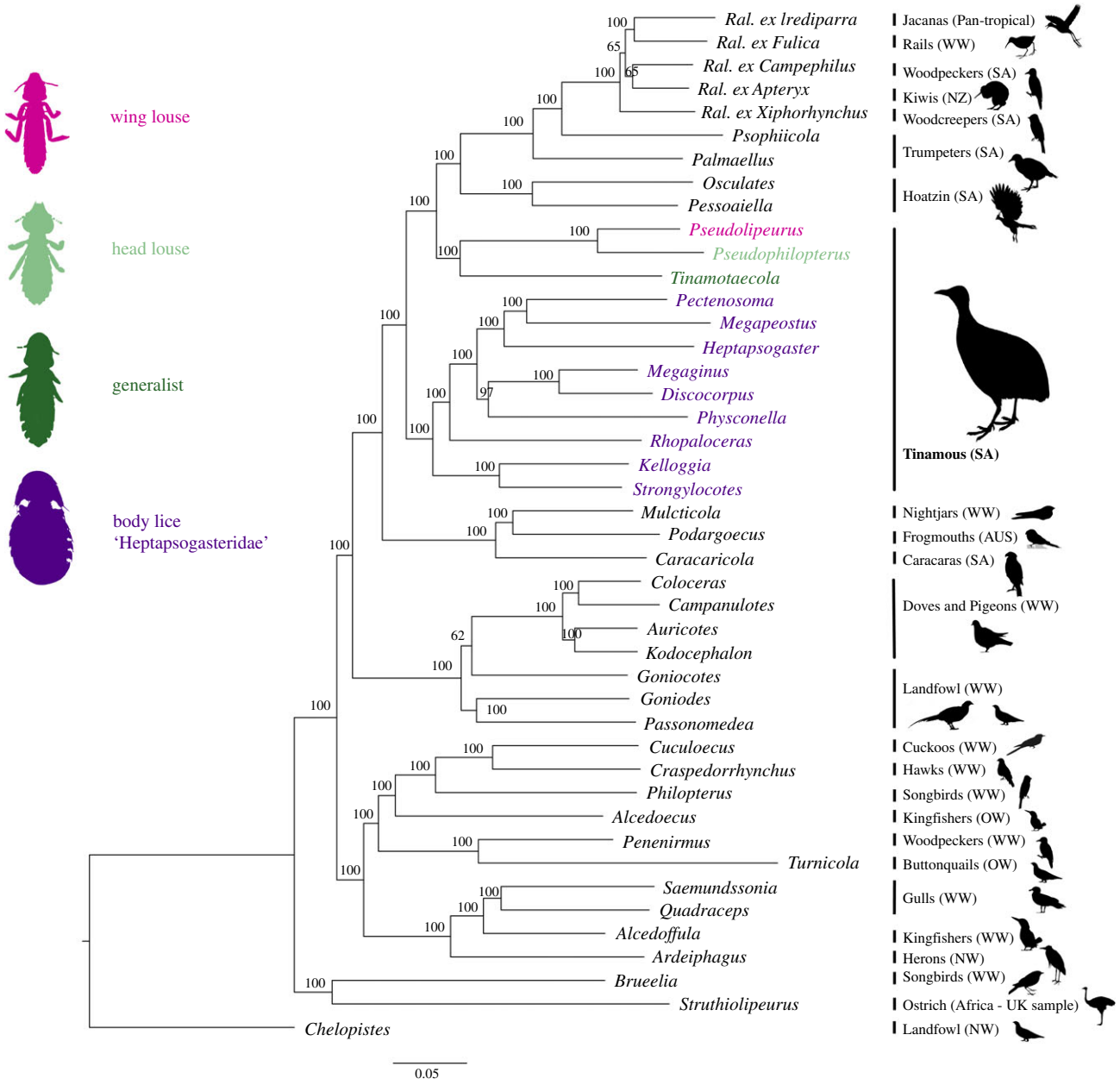

Figure 1. Maximum-likelihood tinamou louse phylogeny, based on a RAxML analysis of the concatenated sequence alignment of 1068 nuclear genes. Tinamou lice are coloured based on ecomorphs as indicated on the left-hand side of the figure. All terminal louse genera are labelled with their avian host group and are with their generalized biogeographic distributions including Old World (OW), New World (NW), South America (SA), Worldwide (WW), Australasia (AUS), and New Zealand (NZ). Bootstrap support values are indicated above each branch, and branch lengths are scaled to nucleotide substitutions per site, as indicated by the scale bar below the phylogeny. *Ral*., *Rallicola*. (For silhouette licences, see electronic supplementary material, table S2.) (Online version in colour.)

doves (Columbiformes) because morphological studies by Smith [27,29] placed these body lice (Goniodidae) close to tinamou body lice (Heptapsogasteridae). However, we found that the lice recovered as sister to the larger clade containing all tinamou lice was a clade comprising the genera *Mulcticola* (from nightjars—Worldwide), *Podargoecus* (from frogmouths—Australasia/SE Asia), and *Caracaricola* (from caracaras—Neotropics) and not the Gonididae (from landfowl, pigeons, and doves) (figure 1).

4. Discussion

Prior phylogenetic studies that included tinamou lice were limited by both taxonomic sampling of this group and in the amount of molecular data available. For example, Johnson *et al*. [10] included some tinamou louse samples, but the molecular and morphological trees were conflicting, and the molecular analyses were limited to only three genes. In our current study, we sequenced the entire genome of lice and assembled 1068 genes for inclusion in a large phylogenomic dataset, which vastly increased the amount of data for this group and increased the certainty of our phylogenetic reconstructions. Furthermore, we substantially improved on prior taxon sampling in our molecular dataset, including 12 genera of tinamou lice (versus at most five in any prior study).

One major goal of our study was to address whether tinamou feather lice form a monophyletic group, to better understand the radiation of lice on this group of hosts and their relationships to other feather lice. Using phylogenomic data derived from whole-genome sequencing, we estimated a higher-level phylogeny of tinamou feather lice and relatives and analysed these data with both concatenated and

coalescent methods. We found that as a whole, tinamou lice are paraphyletic. The group of lice nested phylogenetically within tinamou lice mostly occurs on South American birds from a variety of avian families and orders. The body lice of tinamous (Heptapsogasteridae), which comprises most of the generic diversity of tinamou lice, did form a monophyletic group. Given that we sampled a large fraction of the diversity of tinamou body lice, and that this group has been well characterized in the past by distinct morphological synapomorphies [27], we fully expect that the currently unsampled members of tinamou body lice (Heptapsogasteridae) will fall within this clade. These tinamou body lice were sister to the remainder of this potential *in situ* South American radiation, which also included the head (*Pseudophilopterus*), wing (*Pseudolipeurus*), and generalist (*Tinamotaecola*) tinamou lice.

This new genome-scale dataset has provided new insights into the phylogeny for this group of lice and their relatives and gives hints regarding the origins of this diversity. Tinamous are estimated to have diverged from within ratites around 40 Ma [17]. While they might have inherited their lice from a common ancestor, this also is a long timeframe over which lice might have switched from other birds to tinamous or from tinamous to other birds. The phylogenetic tree of tinamou lice suggests that both processes may have occurred. First, tinamou feather lice as a whole, while relatively closely related, are in a highly derived position among avian feather lice ([32], figure 1), despite the relatively ancient age of tinamous. This implies that tinamou lice were initially derived from lice parasitizing other avian host groups. Secondly, the *in situ* radiation suggests a history of ancient host-switching events in South America from tinamous onto other South American avian hosts. Several dispersal mechanisms exist by which this host-switching might have occurred between tinamous and other avian host groups, including hosts sharing dust baths, dispersal of lice between host species via phoresis on hippoboscid flies, or different species of hosts sharing nesting sites [9].

Tinamous harbour an incredibly rich louse community and thus one major question is how that community was assembled. A number of potential mechanisms may explain the high generic diversity of tinamou lice. A diversifying group of hosts can inherit parasites from their common ancestors, but over evolutionary time new parasites are gained, and old ones can be lost via extinction and speciation [49]. Host and parasite species richness are highly correlated [50]. However, tinamous have a higher than expected parasite richness given the moderate diversity of tinamou species [9,19]. For example, there are 20 genera of lice recorded from 34 species of tinamous (Tinamidae) [7]. By contrast, there are only 4 genera of lice recorded from the 69 species of owls (Strigidae). Likewise, there are only 18 genera of lice recorded from 167 species of land fowl (Phasianidae). Tinamous have relatively low dispersal capabilities and, therefore, their populations remain isolated. This isolation may contribute to tinamou louse diversity. In fact, geographically isolated subspecies of tinamous will often host different species of lice [7]. This isolation may provide increased opportunities for speciation and diversification of these lice over time on their respective host genera and species [9,20]. However, host-switching events can also lead to higher than expected parasite species richness, if gene flow between host species is reduced after the host-switching event, leading to eventual parasite speciation.

The evolutionary age of tinamous [9,20] has also been used as an explanation for why they might host a large diversity of lice. The old age of this host lineage would allow more opportunities for its parasites to speciate. However, both the phylogenetic position of tinamou lice and the fact that ratites, which are just as old as tinamous, have a low diversity of feather lice, suggest that this explanation alone cannot explain this extremely high parasite diversity pattern.

It is important to consider that the body of a bird comprises the entire habitat [50] for these parasites, because they spend most, if not all, of their lives on the body feathers of the bird. A major contributing factor to parasite diversity may be host body size. Generally, larger-bodied hosts have higher parasite diversity [49–54], because either larger birds can support more lice on a per gram basis [49] or because larger birds host a higher abundance of lice overall [55] leading to a decreased extinction risk. This is analogous to the well-established species-area relationships for islands [56]. Compared to many groups of birds, tinamous are relatively large bodied, although they range greatly in size from the 49 g dwarf tinamou (*Taoniscus nanus*) to the 2080 g grey tinamou (*Tinamus tao*) [57]. However, ratites and some other groups of birds have much larger body masses and yet host a relatively smaller diversity of lice. Thus, body size alone is unlikely to explain the extraordinary diversity of tinamou lice.

Another factor that may be important in explaining why tinamous harbour so many louse taxa is the structure of their feathers, because these feathers provide habitat for avian lice. Few living orders of birds have homogeneous feather covering [9], except for some ratite lineages, which lack apteria, areas of bare skin between feathers [58]. Although tinamous are derived from within ratites, they do not have homogeneous feather covering, which may explain why they have so many genera and types of lice in comparison to ratites [9]. It also appears that tinamous are one of the only groups of birds that have downy feathers in the feather tracts but not in the apteria [59,60], which could result in an increased number of isolated niches for feather lice if it is difficult for these parasites to move across the skin between feather tracts.

The phylogeny presented here provides a new framework for understanding the diversity of tinamou lice. Whatever the explanation for the diversity of lice on tinamous, our results indicate that this diversification happened *within* tinamous, and not by repeated host switching from other bird lineages. Specifically, this comprehensive molecular phylogeny of tinamou lice provides evidence that tinamou lice as a whole are more closely related to each other than previously expected. These data also suggest that a radiation of lice within South America originated on tinamous. More in-depth sampling in the future will help further expand the understanding of the pattern of diversification in this understudied group of parasites.

Ethics. Research on animals was conducted according to University of Illinois IACUC protocols 10119, 13121, and 15212.

Data accessibility. Data reported in this paper are deposited in NCBI SRA (see electronic supplementary material, table S1 for Accession Numbers). Concatenated data matrix, gene alignments, gene trees, and all tree files are available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.s1rn8pk4b [61].

Authors' contributions. S.V.H., J.D.W., and K.P.J. designed and coordinated the research. S.V.H., A.D.S., J.M.A., and K.K.O.W. collected

and analysed the data. K.P.J. obtained and selected specimens for the study. J.M.A., J.D.W., and K.P.J. obtained funding and resources for the study. S.V.H. wrote the manuscript and all authors contributed to editing the paper.

Competing interests. We declare we have no competing interests.

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