Impact of forest size on parasite biodiversity: implications for conservation of hosts and parasites
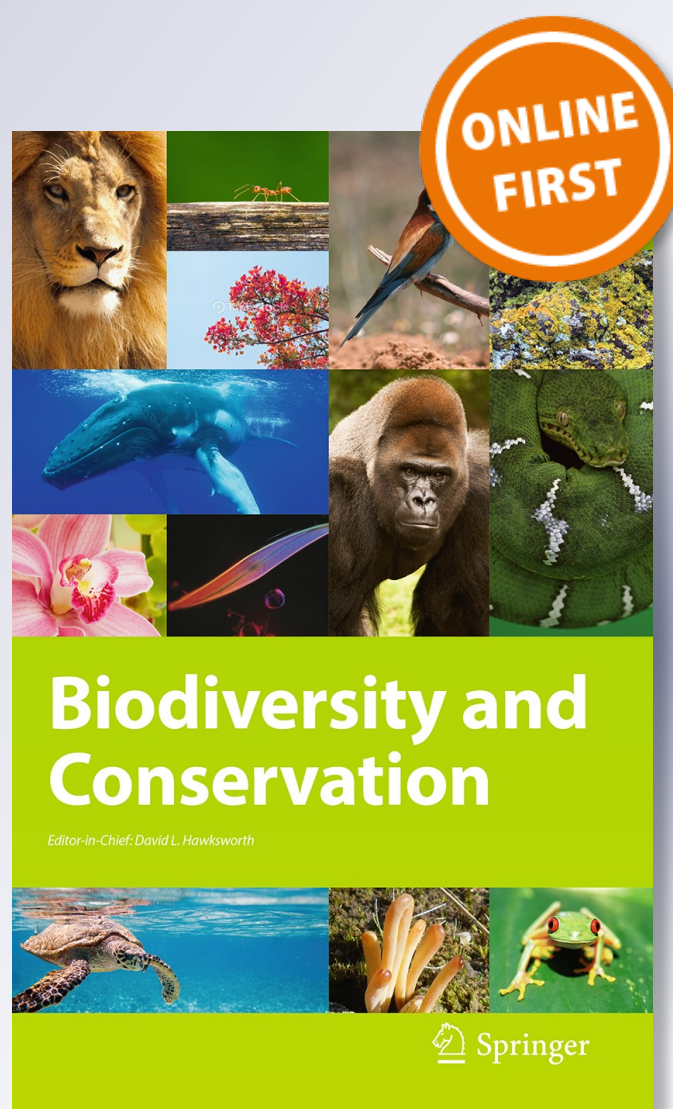
Sarah E. Bush, Michelle Reed & Sean Maher

ONLINE FIRST

Biodiversity and Conservation

Editor-in-Chief: David L. Hawksworth

Springer

Springer

Springer

ORIGINAL PAPER

Impact of forest size on parasite biodiversity: implications for conservation of hosts and parasites

Sarah E. Bush · Michelle Reed · Sean Maher

Abstract Studies of biodiversity traditionally focus on charismatic megafauna. By comparison, little is known about parasite biodiversity. Recent studies suggest that co-extinction of host specific parasites with their hosts should be common and that parasites may even go extinct before their hosts. The few studies examining the relationship between parasite diversity and habitat quality have focused on parasites that require intermediate hosts and pathogens that require vectors to complete their life-cycles. Declines in parasite and pathogen richness in these systems could be due to the decline of any of the definitive hosts, intermediate hosts, or vectors. Here we focus on avian ectoparasites, primarily lice, which are host specific parasites with simple, direct, life-cycles. By focusing on these parasites we gain a clearer understanding of how parasites are linked to their hosts and their hosts' environment. We compare parasite richness on birds from fragmented forests in southern China. We show that parasite richness correlates with forest size, even among birds that are locally common. The absence of some ectoparasite genera in small forests suggests that parasites can go locally extinct even if their hosts persist. Our data suggest that the conservation of parasite biodiversity may require preservation of habitat fragments that are sufficiently large to maintain parasite populations, not just their host populations.

S. E. Bush (✉) · M. Reed
Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
e-mail: bush@biology.utah.edu

Present Address:
M. Reed
University of Michigan, Ann Arbor, MI 48109, USA
e-mail: miche.reed@gmail.com

S. Maher
Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA
e-mail: smaher02@gmail.com

Present Address:
S. Maher
Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

🙆 Springer

Introduction

If you are fortunate enough to stare through binoculars and see a Blue-crowned Laughingthrush (*Garrulax courtoisi*), you will be looking at one of the few remaining individuals of this species (Hong et al. 2003). These birds live in a severely fragmented habitat in southern China and it is not clear how long this critically endangered species will persist (IUCN 2010). Even more uncertain is the fate of the parasites that live inside and on the surface of these birds.

Parasites tend to be host-specific. They are frequently found on only a few, or even a single, host species (Price 1980; Poulin and Morand 2004). Because of this high degree of specificity the co-extinction of parasites with their hosts may be common (Moir et al. 2010). In a study of twenty host-parasite systems, Koh et al. (2004) use models to estimate that 6,300 species are "co-endangered" with their hosts. Recently, Harris and Dunn (2010) found 20-fold as many parasite species on carnivores as there are North American carnivores. Dunn et al. (2009) estimated that the co-extinction rate of these parasites may be as much as tenfold higher than the extinction rate of their hosts. Parasites may even be at risk of extinction before their hosts. In order for parasite populations to persist, a minimum host population is required. This minimum threshold is determined by several factors, including rates of parasite transmission and rates of host and parasite reproduction and mortality (Roberts et al. 2001). In essence, host populations are "islands" and host population size should determine parasite diversity, just as classical island biogeographic theory predicts (Kuris et al. 1980). If the size of the host population drops below a critical threshold then the parasites should go extinct, even if the host persists (Lyles and Dobson 1993; Lafferty et al. 2008).

There is little empirical data about parasite extinctions despite the fact that organisms are rapidly going extinct (Pimm and Raven 2000; Thomas et al. 2004). There are only a few records of extinct parasites (Dunn 2009). Just one parasite, the Pygmy Hog Sucking Louse (*Haematopinus oliveri*), is listed as endangered by the IUCN (Whiteman and Parker 2005; IUNC 2010), despite the fact that nearly two decades ago parasitologists documented >40 tick species at risk of extinction with their hosts (Durden and Keirans 1996). Ticks are among the most studied parasites, yet they represent only a small portion of parasite diversity (Poulin and Morand 2004). The under-representation of parasites among known extinct or endangered organisms is at least partly because parasites have been understudied. It is also possible that current models underestimate the ability of parasites to adapt and exploit new and changing resources, and in so doing overestimate the susceptibility of parasites to extinction (Dunn et al. 2009; Colwell et al. 2012). To predict how habitat destruction will influence parasite diversity, studies investigating the impact of habitat loss on parasites are needed.

A few studies have investigated how vertebrate parasites are influenced by habitat destruction. Altizer et al. (2007) conducted a comparative study using historical parasite records of primates and found that threatened primates harbor fewer parasite species than their non-threatened relatives, suggesting that parasite diversity already has been lost on some primate hosts. In a field study, Vogeli et al. (2011) found that avian pathogen richness was greatest among the largest lark populations, which were found in the largest habitat

patches. Lafferty et al. (2008), found that fishes in pristine reefs have more parasites than fishes from heavily fished areas. These studies, however, are based primarily, if not exclusively, on parasites with complicated life-cycles. Changes in parasite richness in any of these systems could be due to a decrease in the definitive hosts, intermediate hosts or vectors. Studies focused on parasites that rely on only one host to complete their lifecycle should clarify the relationships between parasite diversity, host abundance, and habitat size.

Here we focus on avian ectoparasites, primarily lice, which are host specific parasites with simple, direct, life-cycles. Lice spend their entire life on the body of the bird and transmit to new host individuals during direct contact such as between mates or between parents and offspring in the nest (Clayton and Tompkins 1994). By focusing on these parasites we gain a clearer understanding of how parasites are linked to their hosts and their hosts' environment. We investigated the impact of forest fragmentation on the diversity of avian ectoparasites in southern China. This area (Fig. 1) was once a continuous swathe of tropical and subtropical evergreen forest extending from the southern China coast south to northern Vietnam east of the Red River (Robbins et al. 2006). The remaining forest is highly fragmented as a consequence of centuries of human use (MacKinnon 1997; Myers et al. 2000). Firewood is routinely harvested from these forests and hornbills, parrots, trogans, and woodpeckers that rely on large dead trees for food and nesting holes are rare or absent (Robbins et al. 2006). Not surprisingly, even the more common bird species that
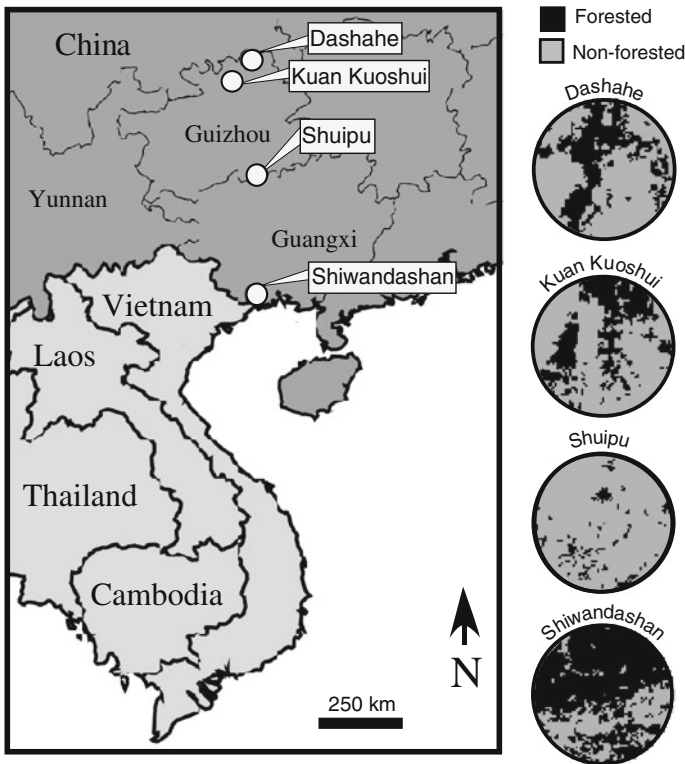

Fig. 1 Biodiversity study areas in southern China. Enlargements of each field site (*right*) indicate the forest cover in a 10 km radius from base camp

persist in these fragmented forests have suffered. Fragmentation frequently leads to a reduction in bird population size (Rolstad 1991; Connor et al. 2000; Lampilla et al. 2005), and we found this to be the case in our study area (Robbins et al. 2006; Boyd et al. 2008; also see "Discussion" section). To determine the effect that forest fragmentation has on parasites, we compared ectoparasite richness from seven genera of birds found among fragmented forests that ranged in size from 0.26 to 215.1 km^2.

Methods

Birds were collected primarily by mist netting and occasionally by shooting. Birds were handled and euthanized according to standard ornithological guidelines (Fair et al. 2010). All birds were placed individually in paper bags prior to processing to prevent ectoparasites from transferring between hosts. After ectoparasites were sampled, the birds were prepared as museum specimens and deposited in the University of Kansas Natural History Museum or in regional museums in southern China.

Parasite sampling method

Ectoparasites were removed from dead birds according to the "post-mortem fumigation" method of Clayton and Drown (2001). We fumigated each bird for at least 15 min in a Tupperware^{TM} container with a cotton ball soaked with ethyl acetate. Ethyl acetate is toxic to arthropods but safe for human use (Clayton and Drown 2001). After fumigation, the bird was removed from the container and held over a cafeteria tray lined with a large sheet of white paper. The Tupperware^{TM} container was searched carefully for ectoparasites, and cleaned between uses. Exposed soft tissue on the face of each bird was examined carefully for attached ectoparasites (e.g. ticks), which were removed with forceps. Next, the bird's feathers were ruffled vigorously over the tray in a series of 'bouts'. For each bout, every feather tract on the bird was thoroughly ruffled. Birds were ruffled for repeated bouts for a minimum of 3 min., or until the bird was ruffled for an entire bout without dislodging any ectoparasites. Tests of this method, calibrated with more rigorous post-mortem ruffling methods (Clayton and Drown 2001) indicate that this sampling procedure accurately accounts for the total number of ectoparasitic fleas, flies, lice and ticks on each bird ($R^2 = 0.99$, $P < 0.0001$, unpublished data), and recovers 97.3 % of all ectoparasite morphospecies, except mites. Thus, mites were not included in this study. All ectoparasites were preserved in vials of ethanol for later counting and morphotyping.

Determination of minimum host sample size

To determine the minimum number of host individuals that needed to be sampled to accurately reflect ectoparasite diversity, we generated ectoparasite accumulation curves from the ten largest "host samples" ($n = 16$–37 host individuals). Host samples included all bird individuals within a genus from a given geographic location. Using a Weibull probability analysis, we calculated that a detection probability of 90 % corresponds with a sample size of 12 host individuals. To compare ectoparasite diversity among sites we therefore restricted analyses to host genera where at least 12 individuals were sampled from each site.

Among site comparisons

Birds were surveyed for ectoparasites at four sites in southern China (Fig. 1; Table 1):

Shiwandashan National Nature Preserve: Guangxi Province, elevation 300–900 m, 21°13′48″N, 107°52′48″E, March–May 2005, total day net hours 5,910. Birds were captured along a winding paved road, through steep mountains of the preserve at roughly 500 m. The forest was entirely secondary with the tallest trees $\sim$25 m (Robbins et al. 2006).

Kuan Kuoshui Nature Preserve: Guizhou Province, elevation 1,450–1,750 m, 28°13′48″N, 107°09′36″E, March–May 2006, total day net hours 1,188. Birds were captured in deciduous and evergreen forests with some trees as tall as $\sim$25 m. The valley floor and surrounding hills were cultivated and streams drained into a small lake on the valley floor (Boyd et al. 2008).

Dashahe Nature Preserve: located in Guizhou Province, elevation 1,350–1,650 m, 29°10′12″N, 107°34′12″E, March–May 2006, total day net hours 1,128. Birds were captured in heavily disturbed natural vegetation at 1,350 m. Maximum height of trees was $\sim$15 m., secondary growth surrounded the valley, much of which was agricultural plots of tobacco, etc. Secondary vegetation surrounded the valley and some native vegetation lined a small river running through the steep karst landscape (Boyd et al. 2008).

Shuipu (near Maolan National Nature Preserve): Guizhou Province, elevation 635–850 m, 25°29′05″N, 107°52′54″E, March–May 2007, total day net hours 6,036. Birds were captured in forests around Shuipu village in gently sloping cultivated valley $\sim$500 m wide and several kilometers long. The valley was surrounded by steep, rugged, karst formations. Perennial streams flowing into valley were diverted to agricultural fields (Boyd et al. 2008).

The forest at each of these sites was characterized using GIS. We used ArcGIS 9.3 (ESRI, Inc. 2009) to create a 10 km buffer around each of the field sites (Ralph et al. 1995; Underhill and Gibbons 2002). Landcover data (downloaded 6 Feb 2009) from Ionia GlobCover were reclassified to reflect three categories: forest, non-forest, and water. "Forest" included terrestrial areas categorized as: $\geq$15 % of 5 m height of broad- or needle-leaved evergreen trees, deciduous, or semi-deciduous forest/woodland, and mosaic forests with 50–70 % cover. The remaining terrestrial areas were considered "non-forest". We overlayed the buffers on the reclassified landcover data to extract appropriate grid cells and then examined fragmentation patterns and spatial characteristics using Fragstats 3.0 (McGarigal et al. 2002). We used a moving window to recognize connected grid cells and identify forest size. Forest fragment size was measured as the largest contiguous patch of forest from which birds were captured. Fragments were defined as distinct units within the landscape matrix, such that the minimum distance between fragments was 1.5 km or the size of a single grid cell. We also determined the percent forest cover within a 10 km radius of each field site. The percentage of forest cover is calculated independently of the number, size, and spatial distribution of forest fragments in a given area.

Results

We sampled ectoparasites from 943 birds representing 38 families, 94 genera and $\sim$150 species. The exact number of host species is uncertain because some species of birds are difficult to tell apart without molecular methods, this is particularly true of warblers in the genera *Phylloscopus* and *Seicrurus* (Olsson et al. 2005). Nearly half (46.7 %) of all birds

Table 1 Forest characteristics, hosts sampled, and the prevalence, abundance, and intensity of lice from four field sites in southern China

Site	Forest Characteristics					Host sample size			Lice		
	Fragmt. size (km²)	Total forest area (km²)	(%)	Temp[a] (°C)	Precip[a] (mm)	n	Spp.[b]	Genera	Prev.	Abun.	Inten.
Shuipu	0.26	24.1	7.7	16.9	1,366	363	78	52	40.2	8.6	21.4
KuanKuoshui	63.5	100.0	31.8	14.8	1,149	231	57	40	45.5	17.2	37.9
Dashahe	85.5	103.3	32.9	12.4	1,312	141	44	35	51.1	25.8	50.6
Shiwandashan	215.1	220.1	70.1	20.5	2,019	208	69	51	47.1	6.5	13.7
Total						943	150	94	44.6	12.8	28.7

[a] Mean annual temperature and precipitation calculated from Hijmans et al. (2005)

[b] The number of host species is approximate because some bird species were difficult identify
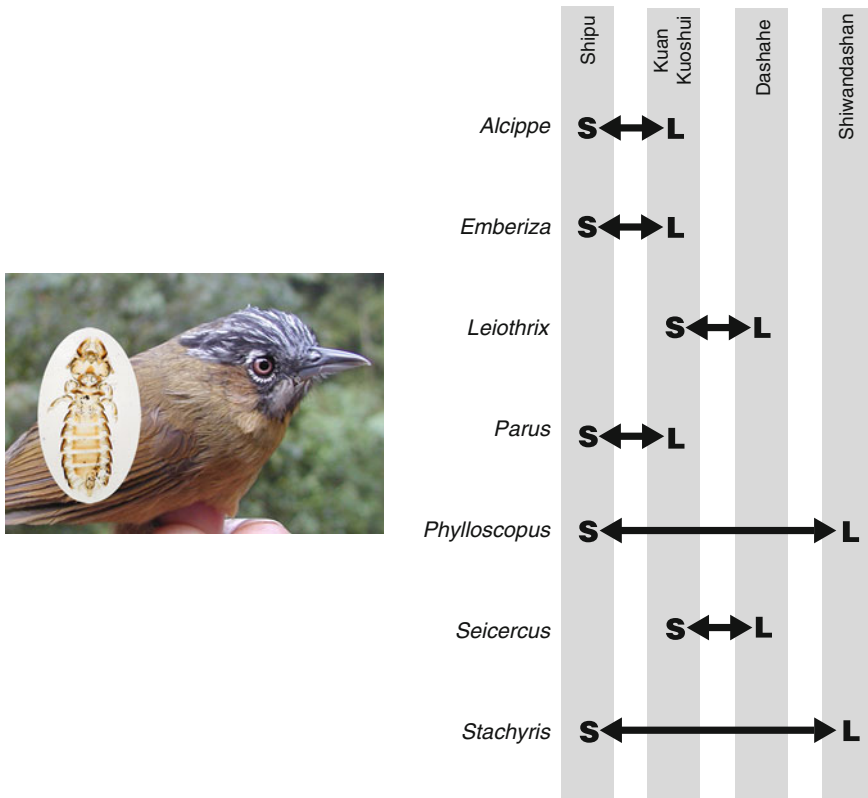
Fig. 2 Among site comparisons are based on seven common host genera that were each sampled at two sites: a relatively *small site* (*S*) and a relatively *large site* (*L*). The four field sites are indicated by *columns* ordered from smallest to largest. *Left* a louse (*Brueelia*, photo by D. Gustafsson) found on babblers (*Stachyris*, photo by A. T. Peterson) in this study

were infested by ectoparasites. Lice were the most common ectoparasites; they infested 44.6 % of all hosts. Other ectoparasites were considerably more rare, with fleas infesting 3.3 %, flies infesting 1.6 %, and ticks infesting 1.1 % of hosts.

Ectoparasites were morphotyped to species, to the best of our ability. The majority of the ectoparasites we collected represent new species or new host records, only some of which have been fully characterized (Price et al. 2006; Hastriter and Bush 2010). Additional taxonomic work is required to make clear species level delineations for most of these ectoparasites. Ecoparasite morphospecies were occasionally found on multiple host species in the same genus. This degree of specificity is common, especially among lice (Price et al. 2003). Thus, our analyses focused on ectoparasite (or louse) species richness with bird genus being the functional taxonomic unit for the hosts.

To understand the impact of forest size on ectoparasite communities we used a restricted data set, which included the seven host genera that were collected from two different field sites in sufficiently large numbers ($n \geq 12$ per site, see "Methods" section for determination of minimum host sample size) to accurately reflect ectoparasite richness. Birds in the other 87 genera were not collected in high enough numbers or they were only collected from one site; consequently, they could not be included in comparative analyses.
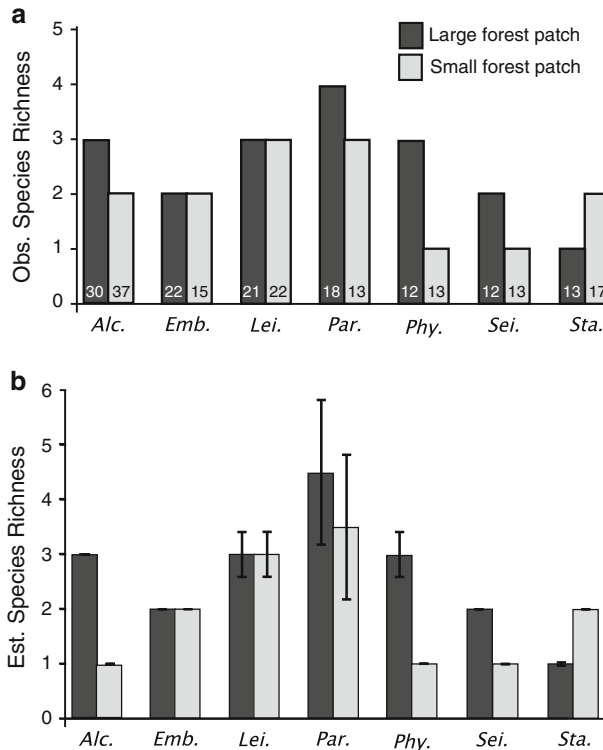
Fig. 3 **a** Observed ectoparasite species richness among the seven bird genera sampled in small and large forests. Numbers in *bars* indicate host sample sizes. **b** Estimated ectoparasite species richness using Chao's (1987) estimator calculated in EstimateS (Colwell 2006). Abbreviations for bird genera are as follows: *Alc. (Alcippe), Emb. (Emberiza), Lei. (Leiothrix), Par. (Parus), Sei. (Seicercus), Sta. (Stachyris)*

Birds were heterogeneously distributed among four field sites; thus, comparisons between sites involved several different combinations of small and large sites (Fig. 2). In this study the bird genera serve as replicates, and comparisons among mixed combinations of small and large sites reduces pseudoreplication between field sites. This design also reduces the influence of potentially confounding factors that differ across sites such as: temperature, precipitations, date of sampling, etc.

The ectoparasite richness we observed ranged from two to five species for each host genus (Fig. 3a; Table 2). In all, we observed 22 host-parasite associations (Table 2). Not all ectoparasites occurred at both small and large field sites; there were 12 cases where an ectoparasite occurred at only one of the two field sites. The majority (67 %) of these localized absences occurred at the smaller field site. We also estimated ectoparasite species richness in EstimateS 8.2.0 (Colwell 2006) using Chao's (1987) estimator, which extrapolates missing taxa from the number of rare taxa in the sample. The Chao (1987) estimator has been evaluated with real and simulated parasite datasets and was found to be a reliable indicator of true parasite taxonomic richness (Walther and Morand 1998, Poulin and Morand 2004). The estimated ectoparasite species richness was very similar to the observed species richness in our study (Fig. 3b).

Table 2 Host-ectoparasite associations for seven host genera sampled at small and large forest sites

Host genera	Parasite morphospecies	Small site	Large site
Alcippe	(L) *Brueelia* sp.	+	+
	(T) *Haemaphysalis* sp.	+	−
	(L) *Menecanthus* sp.	−	+
	(L) *Myrsidea* sp.	−	+
Emberiza	(L) *Brueelia* sp.	+	−
	(L) *Myrsidea* sp.	−	+
	(L) *Ricinus* sp.	+	+
Leiothrix	(F) *Lentistivalius* sp.	+	+
	(L) *Menecanthus* sp.	+	+
	(L) *Philopterus* sp.	+	+
Parus	(F) *Lentistivalius* sp.	−	+
	(L) *Menecanthus* sp.	+	+
	(L) *Philopterus* sp.	+	+
	(L) *Sturnidoecus* sp.	−	+
	(T) *Haemaphysalis* sp.	+	−
Phylloscopus	(L) *Brueelia* sp.	+	+
	(L) *Menecanthus* sp.	−	+
	(L) *Ricinus* sp.	−	+
Seicercus	(L) *Menecanthus* sp.	+	+
	(L) *Philopterus* sp.	−	+
Stachyris	(L) *Brueelia* sp.	+	+
	(L) *Myrsidea* sp.	+	−

Although flies were collected at these sites, no flies were collected from these bird genera

L louse, *T* tick, *F* flea, + indicates parasite was detected at a given site, − indicates that the parasite was not detected

There was a significant effect of forest fragment size on ectoparasite species richness, smaller forest fragments had fewer ectoparasites (GLM, Poisson distribution, Log link, whole model test, df = 13, χ^2 = 37.3, P = 0.0004; effect of forest fragment size, df = 1, χ^2 = 4.1, P = 0.04); this pattern was also significant when differences among host genera were taken into account (interaction effect of forest fragment size and host genus df = 6, χ^2 = 17.3, P = 0.008; effect of host genus, df = 6, χ^2 = 22.2, P = 0.001). Analyses characterizing the forest as the total forested area within a 10 km^2 radius of each site also yielded similar patterns (GLM, Poisson distribution, Log link, whole model test, df = 13, χ^2 = 37.3, P = 0.0004; interaction effect of forest area and host genus df = 6, χ^2 = 17.4, P = 0.008). This similarity is not surprising because forest fragment size and total forested area were highly correlated among the field sites in our study (R = 0.99, P = 0.007).

Most of the ectoparasites observed in this study were lice (lice represent 82 % of the host-parasite associations listed in Table 2). When we restricted analyses to lice we found a slightly stronger effect of forest fragment size on louse species richness. Smaller forest fragments had significantly fewer species of lice (GLM, Poisson distribution, Log link, whole model test, df = 13, χ^2 = 37.7, P = 0.0003; effect of forest fragment size, df = 1, χ^2 = 5.6, P = 0.02); this pattern was also significant when differences among host genera were taken into account (interaction effect of forest fragment size and host genus df = 6,

$\chi^2 = 18.6$, $P = 0.005$; effect of host genus, df = 6, $\chi^2 = 22.3$, $P = 0.001$). Analyses characterizing the forest as the total forested area within a 10 km^2 radius of each site yielded similar patterns (GLM, Poisson distribution, Log link, whole model test, df = 13, $\chi^2 = 37.8$, $P = 0.0003$; interaction effect of forest area and host genus df = 6, $\chi^2 = 18.7$, $P = 0.005$). In addition, the prevalence of lice was greatest among birds in larger forests (MANOVA: interaction effect of forest fragment size (small vs. large) and host genus df = 6, 243, $F = 2.43$, $P = 0.03$), but louse intensity did not differ significantly between hosts in different sized forests (MANOVA: interaction effect of forest fragment size and host genus df = 6, 89, $F = 1.22$, $P = 0.30$, power = 0.94, Effect size $f^2 = 0.15$, Cohen 1988).

Discussion

We investigated the relationship between forest size and ectoparasite species richness and found that birds in smaller forests harbored fewer ectoparasites. Lice were the most common ectoparasites observed in our study, and we also found that birds in smaller forests harbored fewer species of lice. This was true whether forest size was characterized by the size of a forest fragment or by the percentage of forest in an area. To our knowledge, this is the first rigorous demonstration of a correlation between forest size and avian ectoparasite diversity. Strikingly, in our study the correlation between ectoparasite richness and forest size was observed among birds that were common in southern China. Rare and endangered hosts that are restricted to smaller forests are likely to have even more depauperate ectoparasite fauna.

Birds in smaller forests had fewer lice species and a lower prevalence of lice than birds in larger forests. However, the intensity of louse infestations did not differ between birds in different sized forests. It has been hypothesized that hosts experiencing environmental stress may be less able to defend themselves against parasites (Lyles and Dobson 1993; Lafferty and Kuris 1999; Lafferty and Holt 2003). This hypothesis was not supported by our data. It appears that birds in small forests, once they are infested, are able to defend themselves against lice as well as birds in larger forests.

Lice have a simple life-cycle and are typically transmitted directly from host to host during direct physical contact. We also observed ectoparasites with more complex life cycles: fleas and ticks. Fleas have free-living immature stages, and only require vertebrate hosts once they reach the adult stage. Ticks have several developmental stages, with each stage typically feeding on progressively larger vertebrate host species. Interestingly, ticks (*Haemaphysalis* sp.) were only present on hosts at Shuipu, the smallest, most fragmented site. This pattern is markedly different from that of the lice, which were most frequently absent from the smallest forest (Table 2). The occurrence of *Haemaphysalis* sp. on birds at Shuipu could have been a consequence of increased exposure to humans and their domesticated animals, which commonly host these ticks. Studies in North America have shown that habitat fragmentation influences host use by ticks and the pathogens they vector (Allan et al. 2003). Effective conservation strategies for bird populations in small forest fragments may need to account for an increased infestation by generalist parasites such as ticks and pathogens they vector.

The lower ectoparasite richness on birds in small forest fragments could be driven by reduced host abundance. At our study sites, bird abundance was correlated with forest size. On average, across the seven host genera in the study, it took 2.9-fold longer (net hours) to catch 12 birds in small forest sites than in large forest sites (matched pairs, $n = 7$, df = 6,

$t = -2.4$, $P = 0.05$). Historically, birds in these areas were probably more abundant and the increased contact between host individuals could have lead to more widely distributed parasites. However, no historical data exist on the parasite fauna of this region; thus, it is impossible to determine if the absence of parasites in this study is due to geographic specificity or local extinction. Our data are consistent with the possibility of local extinction and the claim that parasite extinctions are an under-represented aspect of lost biodiversity (Koh et al. 2004; Dunn et al. 2009; Moir et al. 2010). Not only do parasites face co-extinction with their hosts, some parasites may face extinction on small host populations of common species. Management strategies that lead to the conservation of minimal host populations may not be large enough to conserve parasite diversity, especially for host-specific parasites. The conservation of parasite biodiversity may require strategic preservation of habitat fragments that are sufficiently large to maintain parasite populations, not just host populations.

Re-colonization of host populations in forest fragments may be difficult. In our study, two of the seven host genera compared among sites are migratory (*Emberiza* and *Phylloscopus*; Peterson et al. 2008). Despite its migratory nature, however, *Phylloscopus* still had reduced ectoparasite species richness in small forests. This suggests that opportunities for parasite transmission during host migration may not be sufficient for parasite re-colonization in this system (but see Malenke et al. 2011). Additional studies are needed to determine how factors such as host specificity, parasite transmission, and host movement either between forest gaps or across migratory routes can influence parasite re-colonization.

The observed pattern between ectoparasite species richness and forest size is particularly striking, given that the maximum number of ectoparasite species detected on any host genus in this study was only five. This is likely an underestimate of the actual ectoparasite diversity on these birds for several reasons: rare parasites could have gone undetected, mobile parasites like fleas and flies may have left their hosts before they were removed from mist nets, and some suites of ectoparasites such as quill, skin, and feather mites were ignored because we could not quantify them accurately in the field. None of these issues bias the interpretation of the observed data because sampling methods were the same across host genera and field sites. In the future, however, studies investigating the relationship between forest size and additional parasite taxa would be informative. For example, mites are especially diverse; a single parrot species (*Aratinga holochlora*) is known to be infested by at least 25 species of feather mites, and probably hosts several species of skin mites, nest mites, quill mites, and nasal mites (Perez 1995, 1997). Studies incorporating a more diverse assemblage of parasites may be able to detect more subtle differences in the relationship between forest size and parasite diversity.

Our data suggest that the diversity of host specific ectoparasites may be a useful indicator of host diversity. Recent studies of marine and estuary systems show that parasite diversity reflects host diversity (Hechinger and Lafferty 2005; Hechinger et al. 2007, 2008; Lafferty et al. 2008) and that parasites can be used as indicators of ecosystem health (Hudson et al. 2006). The parasites studied in these systems typically have complex life cycles that require several different host species. Population declines in the definitive hosts or any of the intermediate hosts could lead to a decrease in parasite richness in these systems. Consequently, parasites with complex life cycles may serve as general indicators of ecosystem health but they may not be useful as indicators of the size or health of any particular host species. On the other hand, ectoparasites like lice are highly host specific, permanent parasites that complete their entire life cycle on the body of a single host species. These ectoparasites may prove to be a powerful bioindicators of the status of host

populations. Importantly, ectoparasites can be sampled easily without harming the host (Clayton and Drown 2001), and sampling ectoparasites can be more efficient than conducting time intensive surveys throughout a forest to directly quantify host population size (Ralph et al. 1995; Rosenstock et al. 2002). The relative diversity of ectoparasite species among hosts in different habitats, or over time, should indicate the relative size of the host populations. Sharp declines in parasite species richness over time may forewarn wildlife managers of host population declines. In essence, fewer parasites on the "canaries in the coal mine" may portend a decline in host biodiversity.

References

Allan BF, Keesing F, Ostfeld RS (2003) Effects of habitat fragmentation on Lyme disease risk. Conserv Biol 17:267–272

Altizer S, Nunn CL, Lindenfors P (2007) Do threatened hosts have fewer parasites? A comparative study in primates. J Anim Ecol 76:301–314

Boyd RL, Nyari AS, Benz BW, Chen G (2008) Aves, province of Guizhou, China. Check List 4:107–114

Chao A (1987) Estimating the population size for capture-recapture data with unequal catchability. Biometrics 43:783–791

Clayton DH, Drown DM (2001) Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). J Parasitol 87:1291–1300

Clayton DH, Tompkins DM (1994) Ectoparasite virulence is linked to mode of transmission. Proc Roy Soc Lond B 256:211–217

Cohen J (1988) Statistical power analysis for the behavioral sciences, 2nd edn. Lawrence Erlbaum, New Jersey

Colwell RK (2006) EstimateS: Statistical estimation of species richness and shared species from samples. V.8.2.0. purl.oclc.org/estimates

Colwell RK, Dunn RR, Harris NC (2012) Coextinction and extinction cascadees. Ann Rev Ecol Evol Syst 43:183–203

Connor EF, Courtney AC, Yoder JM (2000) Individuals-area relationships: the relationship between animal population density and area. Ecol 81:734–748

Dunn RR (2009) Coextinction: anecdotes, models and speculation. In: Tuvey ST (ed) Holocene extinctions. Oxford University Press, Oxford, pp 167–180

Dunn RR, Harris NC, Colwell RK, Koh LP, Sodhi NS (2009) The sixth mass coextinction: are most endangered species parasites and mutualists? Proc Roy Soc Lond B 276:3037–3045

Durden LA, Keirans JE (1996) HostParasite coextinction and the plight of tick conservation. Am Entomol 42:87–91

ESRI, Inc.: Environmental Systems Research Institute (2009) ArcGIS: Geographic information software, version 9.3. Redlands, California

Fair J, Paul E, Jones J (2010) Guidelines to the use of wild birds in research, 3rd edn. Ornithological Council, Washington, D.C.

Harris NC, Dunn RR (2010) Using host associations to predict spatial patterns in the species richness of the parasites of North American carnivores. Ecol Lett 13:1411–1418

Hastriter MW, Bush SE (2010) Notes and new records of Fleas (Insecta: Siphonaptera) from small mammals and birds collected in Southern China. Proc Entomol Soc Wash 112:214–228

Hechinger RF, Lafferty KD (2005) Host diversity begets parasite diversity: bird final hosts and trematodes in snail intermediate hosts. Proc Roy Soc Lond B 272:1059–1066

Hechinger RF, Lafferty KD, Huspeni TC, Brooks AJ, Kuris AM (2007) Can parasites be indicators of free-living diversity? Relationships between species richness and the abundance of larval trematodes and of local benthos fishes. Oecologia 151:82–92

Hechinger RF, Lafferty KD, Kuris AM (2008) Trematodes indicate animal biodiversity in the Chilean Intertidal and Lake Tanganyika. J Parasitol 94:966–968

Hijmans RJ, Cameron S, Parra J (2005) WorldClim—global climate data. http://www.worldclim.org. Accessed 8 July 2009

Hong Y, He F, Wirth R, Melville D, Pan-ji Z, Xia-zhi W, Gui-fu W, Zhi-yong L (2003) Little-known Oriental bird: Courtois's Laughingthrush *Garrulax galbanus courtoisi*. Orient Bird Club Bull 38:35–40

Hudson PJ, Dobson AP, Lafferty KD (2006) Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol 21:381–385

IUCN: International Union for Conservation of Nature (2010) *Garrulax courtoisi* in IUCN (2010) IUCN red list of threatened species. Version 2010.3. http://www.iucnredlist.org. Accessed 1 Oct 2012

Koh LP, Dunn RR, Sodhi NS, Colwell RK, Proctor HC, Smith VS (2004) Species coextinctions and the biodiversity crisis. Science 305:1632–1634

Kuris AM, Blaustein AR, Alio JJ (1980) Hosts as Islands. Am Nat 116:570–586

Lafferty KD, Holt RD (2003) How should environmental stress affect the population dynamics of disease? Ecol Lett 6:654–664

Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. Limnol Oceanogr 44:925–931

Lafferty KD, Shaw JC, Kuris AM (2008) Reef fishes have higher parasite richness at unfished Palmyra Atoll compared to fished Kiritimati Island. EcoHealth 5:338–345

Lampilla P, Mönkkönen M, Desrochers A (2005) Demographic responses by birds to forest fragmentation. Conserv Biol 19:1537–1546

Lyles AM, Dobson AP (1993) Infectious disease and intensive management: population dynamics, threatened hosts, and their parasites. J Zoo Wildl Med 3:315–326

MacKinnon J (1997) Protected areas systems review of the Indo-Malayan realm. Asian Bureau for Conservation, Canterbury

Malenke JR, Newbold N, Clayton DH (2011) Condition-specific competition governs the geographic distribution and diversity of ectoparasites. Am Nat 177:522–534

McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial pattern analysis program for categorical maps. www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed 6 Feb 2009

Moir ML, Vesk PA, Brennan KEC, Keith DA, Hughes L, McCarthy MA (2010) Current constraints and future directions in estimating coextinction. Conserv Biol 24:682–690

Myers N, Mittermeier RA, Mittermeier CG, da Fonesca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Olsson U, Alström P, Ericson PGP, Sundberg P (2005) Non-monophyletic taxa and cryptic species—evidence from a molecular phylogeny of leaf-warblers (*Phylloscopus*, Aves). Mol Phylo Evol 36:261–276

Pérez TM (1995) Seven species of Fainalges Gaud and Berla (Analgoidea, Xolalgidae) from *Aratinga holochlora* (Sclater) (Aves, Psittacidae). Zoo Scripta 24:203–223

Pérez TM (1997) Eggs of feather mite congeners (Acarina: Pterolichidae, Xolalgidae) from different species of new world parrots (Aves, Psittaciformes). Int J Acarol 23:103–106

Peterson AT, Bush SE, Spackman E, Swayne DE, Ip H (2008) Influenza A virus infections in land birds, People's Republic of China. Emerg Infect Dis 14:1644–1646

Pimm SL, Raven P (2000) Extinction by numbers. Nature 403:843–845

Poulin R, Morand S (2004) Parasite biodiversity. Smithsonian Institution Scholarly Press, Washington D.C.

Price PW (1980) Evolutionary biology of parasites. Princeton University Press, Princeton

Price RD, Hellenthal RA, Palma RL, Johnson KP, Clayton DH (2003) The chewing lice: world checklist and biological overview. Illinois Natural History Survey Special Publication 24, 501 pp

Price RD, Arnold DC, Bush SE (2006) Five new species of *Myrsidea* (Phthiraptera: Menoponidae) from Asian Babblers (Passeriformes: Timaliidae). J Kansas Entomol Soc 79:369–377

Ralph CJ, Sauer JR, Droege S (1995) Monitoring bird populations by point counts. U.S. Department of Agriculture, Forest Service, General Technical Report PSW-149

Robbins MB, Peterson AT, Nyari AS, Chen G, Davis TJ (2006) Ornithological surveys of two reserves in Guangxi province, China, 2004–2005. Forktail 22:140–146

Roberts MG et al (2001) Parasite community ecology and biodiversity. In: Hudson PJ, Rizzoli A, Grenfell BT, Heesterbeek H, Dobson AP (eds) The ecology of wildlife diseases. Oxford University Press, Oxford, pp 63–82

Rolstad J (1991) Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biol J Linn Soc 42:149–163

Rosenstock SS, Anderson DR, Giesen KM, Leukering T, Carter MF (2002) Landbird counting techniques: current practices and an alternative. Auk 119:46–53

Thomas JA et al (2004) Comparative losses of British butterflies, birds and plants and the global extinction crisis. Science 303:1879–1881

Underhill LG, Gibbons DW (2002) Mapping and monitoring bird populations: their conservation uses. In: Norrisand K, Pain DJ (eds) Conserving bird biodiversity: general principles and their application. Cambridge University Press, Cambridge, pp 34–60

Vogeli MJ, Lemus A, Serrano D, Blanco G, Tella JL (2011) An island paradigm on the mainland: host population fragmentation impairs the community of avian pathogens. Proc Roy Soc Lond B. doi: 10.1098/rspb.2010.1227

Walther BA, Morand S (1998) Comparative performance of species richness estimation methods. Parasitol 116:395–405

Whiteman NK, Parker PG (2005) Using parasites to infer host population history: a new rationale for parasite conservation. Anim Conserv 8:175–181