

THE INFLUENCE OF HOST BODY SIZE AND FOOD GUILD ON PREVALENCE AND MEAN INTENSITY OF CHEWING LICE (PHTHIRAPTERA) ON BIRDS IN SOUTHERN CHINA

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KEY WORDS ABSTRACT

Phthiraptera Ischnocera Amblycera New Records China New Host Records Prevalence Intensity	Chewing lice (Insecta: Phthiraptera) are abundant ectoparasites of birds and mammals. They are adapted to life in the plumage or pelage of their hosts and virtually never leave the host during their life cycle. Most species are highly host specific. This study was carried out to determine species richness, abundance, and prevalence of chewing lice of wild forest birds in the southern region of China. Between July 2012 and June 2016, 2,210 birds (belonging to 8 orders, 45 families, and 215 species) were captured by mist nets and examined for chewing lice. In total, 622 birds of 117 species were parasitized by lice belonging to 89 species in 25 genera from 2 suborders (Amblycera and Ischnocera). Of these, 28 louse species represent new host–louse records for China and 10 worldwide. Chewing louse prevalence varied significantly among host species. There was no evidence of a correlation between climate zones and louse prevalence, but host guild affected prevalence significantly, with insectivorous birds having the lowest prevalence. Louse prevalence was positively correlated with host body mass and bill length, but mean intensity was only correlated with host body mass. These findings contribute further knowledge of avian chewing lice.
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Parasitism is a successful way of life, with about 50% of all known animal and plant species being parasites, representing a large fraction of the earth's biodiversity (Price, 1980; de Meeûs and Renaud, 2002). A principal cause of this diversity is the fact that many parasites are fairly host specific, using only a subset of the hosts available at a given location (Poulin, 2007). Parasites influence almost every aspect of their host's life history. Chewing lice (Insecta: Phthiraptera) are parasitic insects found on virtually all bird and many mammal species (Marshall, 1981). Chewing lice are obligate, permanent ectoparasites with a direct life cycle spent entirely on the body of the host (Brooke, 2010). So far, more than 6,300 chewing louse species have been described, but only around 4,500 of them were accepted as valid by the most recent checklist (Price et al., 2003). Many species of chewing lice exhibit a high degree of host specificity and are important models of host–parasite coevolution on many taxonomic levels (Clayton and Moore, 1997; Clayton et al., 2003; Johnson et al., 2011, 2012; Sweet et al., 2016, 2017, 2018).

Until recently, the study of chewing lice in China has been largely neglected. Previous studies of lice from Chinese hosts have been mainly from caged birds, especially in zoos, mainly focusing on classification with little consideration being given to ecological aspects of the host–parasite relationship. Some chewing lice from

China have been recorded from domestic birds by Yang et al. (1988), and others have been described as new species by Liu (1989a, 1989b, 1990, 1994) from order Galliformes. Huang (2003) published a list of 347 species of bird lice from Fujian Province, China, but he did not include the names of the hosts and only quoted 4 references from which he obtained all the records. Moreover, the list of lice records published by Huang (2003) does not include any specific collection data, nor any data on where these lice are deposited or how they were identified. This list is therefore of dubious authenticity, and many records on this list may be spurious, being derived from a host checklist and the assumption that all lice recorded on these hosts occur in Fujian, rather than on existing lice. We refer to this list here only as a tentative baseline. A few more recent studies on lice from Chinese wild birds have been carried out by foreign authors (e.g., Price et al., 2006; Bush et al., 2013; Gustafsson et al., 2018a, 2018b).

One important factor often overlooked when examining ectosymbiont diversity is the impact of the host's abiotic environment (Malenke et al., 2011). In particular, bird-associated arthropod diversity can be influenced by many climatic factors (Merino and Potti, 1996; Møller, 2010). Unlike endosymbionts, which inhabit more stable environments regulated by host physiology, ectosymbionts, such as chewing lice, can be influenced



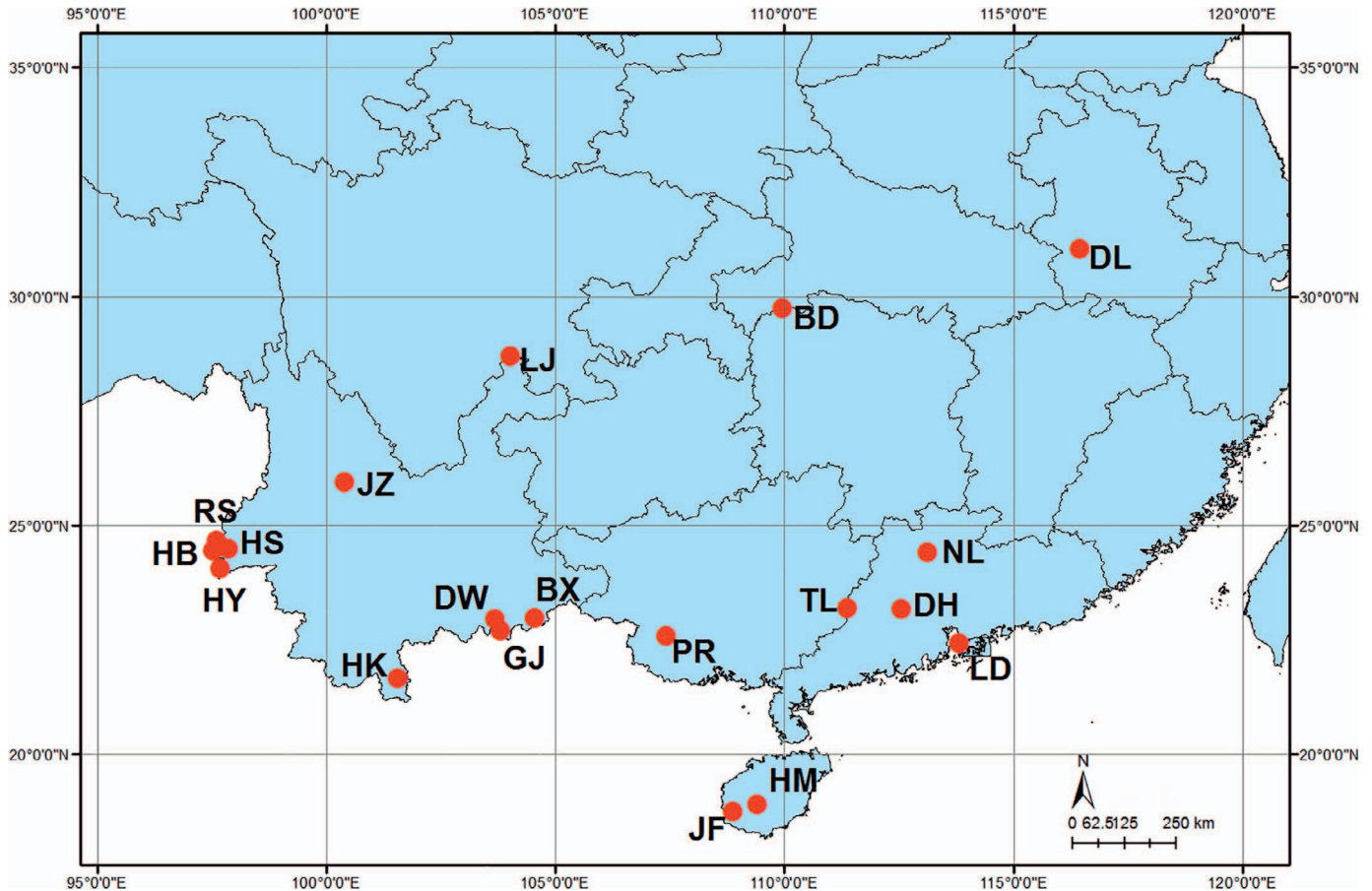


Figure 1. Nineteen sampling sites across southern China. BD, Badagongshan; BX, Baixian; DH, Dinghushan; DL, Dingling; DW, Daweishan; GJ, Gaojingliang; HB, Hongbenghe; HK, Huikuan; HM, Houmiling; HS, Husa; HY, Huyu; JF, Jianfengling; JZ, Jizushan; LD, Lingdingdao; LJ, Laojunshan; NL, Nanling; PR, Pairutun; RS, Rongshuwang; TL, Tongledashan. Color version available online.

by variation in ambient temperature and humidity (Janovy et al., 1997; Moyer et al., 2002a; Møller, 2010). For example, Moyer et al. (2002a) found that ambient humidity had a highly significant impact on louse prevalence and abundance, and Bush et al. (2009) found that this impact may differ between different louse species on the same host.

Bird beaks play an important role in preening, the first line of defense against harmful ectoparasites such as chewing lice, fleas, bugs, flies, ticks, and feather mites (Clayton et al., 2005, 2010). Furthermore, beak size and shape are often closely adapted to the particular food resource available in the bird's environment (Gosler, 1987; Moyer et al., 2002b). Host body mass can also influence the diversity of chewing lice. Larger bodied hosts provide more resources and therefore support larger populations of ectosymbionts (Poulin and Rohde, 1997; Poulin, 2007). For example, Clayton and Walther (2001) found that chewing lice abundance was positively correlated with host body mass across 52 species of Peruvian birds.

Considering the scarcity of published research on lice from China, additional data on the parasitological parameters of chewing lice on wild birds is needed. Therefore, the aims of this study were to (1) gather new data regarding the species richness and distribution of chewing lice on wild forest birds in China; (2) provide information on their prevalence, intensity, and abun-

dance; (3) test whether variation in climate zones and food guilds shape chewing louse communities of wild birds; and (4) test how host morphology may affect diversity of chewing lice (prevalence and intensity) among birds.

MATERIALS AND METHODS

Study sites and birds

The collection of lice was carried out between July 2012 and June 2016 at 19 study sites across southern China (Fig. 1; Table I). We limited this study to the northern subtropics, marginal tropics, south subtropical, and mid-subtropics, representing 4 different climate zones according to the Climate Regionalization Map of China during the period 1981–2010 (Zheng et al., 2013).

We captured birds alive using mist nets, placed each bird in individual cotton bags for a short time, and subsequently examined them individually to collect their ectoparasites. To avoid cross-contamination of samples, a cloth bag was used for each bird sampled. These cloth bags were later washed and inspected before re-use. The bird taxonomy used in this paper follows the International Ornithological Congress World Bird List (Gill and Donsker, 2016). In total, 2,210 birds belonging to 215 species from 45 families and 8 orders were examined for ectoparasites. For statistical analysis, we divided the birds into

Table I. Sampling sites with louse data for each site.

Sampling site*	Latitude	Longitude	Climate zone	n†	Chewing louse prevalence (%)
Dingling (DL)	31°2'N	116°27'E	Northern subtropics	66	13.6
Houmiling (HM)	18°54'N	109°25'E	Marginal tropics	73	21.9
Jianfengling (JF)	18°45'N	108°52'E	Marginal tropics	81	39.5
Huikuan (HK)	21°39'N	101°33'E	Marginal tropics	92	22.8
Daweshan (DW)	22°57'N	103°41'E	Marginal tropics	72	22.2
Baixian (BX)	22°42'N	103°48'E	Marginal tropics	79	19.0
Gaojingliang (GJ)	22°58'N	104°33'E	Marginal tropics	100	16.0
Lingdingdao (LD)	22°25'N	113°49'E	South subtropical	9	44.4
Tongledashan (TL)	23°12'N	111°23'E	South subtropical	176	29.5
Dinghushan (DH)	23°10'N	112°33'E	South subtropical	147	38.1
Pairutun (PR)	22°35'N	107°25'E	South subtropical	128	36.7
Husa (HS)	24°29'N	97°52'E	South subtropical	177	9.6
Huyu (HY)	24°3'N	97°41'E	South subtropical	238	35.3
Hongbenghe (HB)	24°27'N	97°32'E	South subtropical	175	36.0
Rongshuwang (RS)	24°40'N	97°36'E	South subtropical	200	41.0
Nanling (NL)	24°25'N	103°8'E	Mid-subtropics	150	28.0
Badagongshan (BD)	29°44'N	109°58'E	Mid-subtropics	87	13.8
Laojunshan (LJ)	28°42'N	104°1'E	Mid-subtropics	72	37.5
Jizushan (JZ)	25°57'N	100°24'E	Mid-subtropics	88	12.5
Total				2,210	28.1

* Abbreviations for sampling sites are included to enable cross-reference with map in Figure 1.

† Number of examined birds.

resident and migrating species (Zheng, 2011; Richard and Zou, 2015). Birds species were also classified into 6 food guilds based on diet (Zhao, 2001; Zou and Chen, 2004; Wilman et al., 2014), but we did not analyze carnivore, granivorous, and nectarivorous species because sample sizes were too small. Data on bird body mass and bill length are from Wilman et al. (2014) and Zhao (2001) (Suppl. Data, Table S1).

Collection, processing, and identification of lice

All birds were deloused using a standardized method. Lice were collected by using the fumigation chamber method with visual search of the head as described by Clayton and Walther (1997) and Clayton and Drown (2001) and also by visual examination and ruffling of the feathers. Birds were subsequently released into the wild. The detached lice were picked up with fine brushes and transferred to vials with 96% alcohol and stored in the laboratory until they were slide mounted in the laboratory for subsequent microscopic examination. At the same time, collection data for each bird species and the lice collected from them were recorded.

Some lice were slide mounted in Canada balsam as permanent slides, following the technique in Palma (1978), and some were mounted in Hoyers medium (Cielecka et al., 2009), using a dissecting microscope. Genus and species identifications were made under an Eclipse 80i digital microscope (Nikon Corporation, Tokyo, Japan). Identifications of louse genera were carried out primarily using keys in Price et al. (2003). Subsequently, more detailed identifications were made using relevant published information on the genera involved. The scientific names of chewing lice used in this paper follow those in the world checklist by Price et al. (2003), supplemented by names published after 2003 (references listed in Table II for taxa named after 2003). Slide-mounted specimens have been deposited in the collection of

the Guangdong Institute of Applied Biological Resources (Guangzhou, China).

A relatively large number of louse samples were identified to the generic level only, especially those belonging to genera parasitizing species of order Passeriformes (see Table II, given as *Genus* sp.). This lack of species identifications is likely due to several main reasons: (1) inadequate samples, containing only nymphs or one sex; (2) very small samples or samples in poor condition; (3) lack of published revisional studies of the genus involved; and (4) the samples represent new, undescribed species. We have used the term *sensu lato* to denote populations with a range of measurement and morphological variation at present considered different from the named species, but not sufficiently distinct to warrant the erection of separate taxa (Pilgrim and Palma, 1982). We have given numbers to several unidentified species that we believe may represent undescribed species. Further research is planned to describe these species. In the references below, we have not included citations to papers where species listed in Table II were described before 2003, because those citations can be found in Price et al. (2003). However, we have included citations to species described in 2003 and later.

The following louse parameters were evaluated: (1) prevalence: the proportion of the members of a host taxon infested with lice; (2) mean intensity: the number of chewing lice per host among infested hosts; and (3) mean abundance: the number of chewing lice per host among examined hosts (Bush et al., 1997; Sychra et al., 2011).

Statistical analyses

The prevalence, mean intensity, and mean abundance of infestation of chewing lice from each host were calculated for all bird species. All data were examined for normality using Kolmogorov–Smirnov tests. To assess whether the prevalence

Table II. Louse taxa collected on some avian hosts from southern China. Sequences of species follow Gill and Donsker (2016). Note that *Brueelia oxyrhyncha* Gustafsson, Chu, Bush, and Zou, 2018, was described as a new species during the review of this paper. This species was described based on material collected during our study. We therefore count this as a new record for China and a new host record, despite the name having been published before the publication of the present study.

Bird species	Bird common name	Louse species	Louse no.
<i>Lophura nycthemera</i>	Silver pheasant	<i>Amyrsidea subaequale</i> (Piaget, 1880)	4
		<i>Goniocotes albidus</i> Giebel, 1874*	2
		<i>Goniodes cervinicornis</i> Giebel, 1874	7
<i>Chalcophaps indica</i>	Emerald dove	<i>Coloceras piriformis</i> (Tendeiro, 1969)*	32
		<i>Coloceras neoindicum</i> Price, Hellenthal and Palma, 2003*	1
		<i>Columbicola guimaraesi</i> Tendeiro, 1965*	42
<i>Hierococcyx sparverioides</i>	Large hawk-cuckoo	<i>Cuculicola</i> sp. 1	15
<i>Otus lettia</i>	Collared scops owl	<i>Kurodaia deignani</i> Emerson and Elbel, 1960	2
<i>Glaucidium brodiei</i>	Collared owl	<i>Kurodaia deignani</i> Emerson and Elbel, 1960	1
		<i>Strigiphilus heterogenitalis</i> Emerson and Elbel, 1957*	1
<i>Halcyon coromanda</i>	Ruddy kingfisher	<i>Alcedoecus mystacinus</i> (Nitzsch, 1866)*	1
<i>Nyctornis athertoni</i>	Blue-bearded bee-eater	<i>Aporisticeras athertona</i> Williams, 1981*	5
<i>Megalaima asiatica</i>	Blue-throated barbet	<i>Traihoriella binhchhausensis</i> Najer and Sychra, 2014 (in Najer et al., 2014) sensu lato*	2
		<i>Penenirmus</i> sp. 1	4
		<i>Penenirmus pici</i> (Fabricius, 1798) sensu lato*	4
<i>Picus canus</i>	Grey-headed woodpecker	<i>Penenirmus pici</i> (Fabricius, 1798) sensu lato*	10
<i>Blythipicus pyrrhotis</i>	Bay woodpecker	<i>Myrsidea</i> sp. 1	15
<i>Psarisomus dalhousiae</i>	Long-tailed broadbill	<i>Psammonirmus lunatipectus</i> Gustafsson and Bush, 2017 (in Gustafsson and Bush, 2017)	10
<i>Serilophus lunatus</i>	Silver-breasted broadbill	<i>Myrsidea palmi</i> Hellenthal and Price, 2003 (in Hellenthal and Price, 2003) sensu lato*	40
<i>Hemipus picatus</i>	Bar-winged flycatcher-shrike	<i>Philopterus</i> sp. 1	2
<i>Tephrodornis virgatus</i>	Large woodshrike	<i>Philopterus</i> sp. 1	3
<i>Pericocotus brevirostris</i>	Short-billed minivet	<i>Philopterus</i> sp. 2	1
<i>Erpornis zantholeuca</i>	White-bellied erpornis	<i>Ricinus dolichocephalus</i> (Scopoli, 1763) sensu lato*†	1
<i>Pteruthius aeralatus</i>	Blyth's shrike babbler	<i>Myrsidea</i> sp. 2	2
<i>Pteruthius melanotis</i>	Black-eared shrike babbler	<i>Guimaraesiella</i> sp. 1	1
<i>Dicrurus aeneus</i>	Bronzed drongo	<i>Menacanthus eurysternus</i> (Burmeister, 1838)†	2
<i>Dicrurus remifer</i>	Lesser racket-tailed drongo	<i>Guimaraesiella sexmaculata</i> (Piaget, 1880)*	4
<i>Rhipidura albicollis</i>	White-throated fantail	<i>Brueelia rhipidura</i> (Thompson, 1941)*	9
		<i>Ricinus mugimaki</i> (Uchida, 1915)*†	10
<i>Hypothymis azurea</i>	Black-naped monarch	<i>Guimaraesiella</i> sp. 2	2
<i>Terpsiphone incei</i>	Amur paradise flycatcher	<i>Guimaraesiella</i> sp. 3*	1
		<i>Philopteroides terpsiphoni</i> Najer and Sychra, 2012 (in Najer et al., 2012)*	2
<i>Urocissa erythroryncha</i>	Red-billed blue magpie	<i>Olivinirmus husaini</i> (Ansari, 1956)*	5
<i>Cissa hypoleuca</i>	Indochinese green magpie	<i>Olivinirmus</i> sp. 1	7
<i>Parus major</i>	Great tit	<i>Menacanthus sinuatus</i> (Burmeister, 1838)	3
<i>Spizixos semitorques</i>	Collared finchbill	<i>Philopteroides kayanobori</i> (Uchida, 1948)*	2
<i>Pycnonotus sinensis</i>	Light-vented bulbul	<i>Myrsidea gieferi</i> Hellenthal and Price, 2003 (in Hellenthal and Price, 2003)	3
		<i>Menacanthus eurysternus</i> (Burmeister, 1838)	2
<i>Pycnonotus cafer</i>	Red-vented bulbul	<i>Brueelia alophoixi</i> Sychra et al. 2009 (in Sychra et al., 2009)*†	32
<i>Alophoixus flaveolus</i>	White-throated bulbul	<i>Menacanthus orioli</i> Blagoveshchensky, 1951*†	4
		<i>Myrsidea</i> sp. 3	3
		<i>Philopteroides flavala</i> Najer and Sychra, 2012 (in Najer et al., 2012)*†	4
		<i>Myrsidea ochracei</i> Hellenthal and Price, 2003 (in Hellenthal and Price, 2003)*	2
<i>Alophoixus pallidus</i>	Puff-throated bulbul	<i>Philopteroides flavala</i> Najer and Sychra, 2012 (in Najer et al., 2012)*	3
		<i>Brueelia alophoixi</i> Sychra et al. 2009 (in Sychra et al., 2009) sensu lato*	4
		<i>Myrsidea ochracei</i> Hellenthal and Price, 2003 (in Hellenthal and Price, 2003)*	8
<i>Hemixos flavala</i>	Ashy bulbul	<i>Philopteroides flavala</i> Najer and Sychra, 2012 (in Najer et al., 2012)*†	5
<i>Hemixos castanonotus</i>	Chestnut bulbul	<i>Brueelia alophoixi</i> Sychra et al. 2009 (in Sychra et al., 2009) sensu lato*†	7
		<i>Philopteroides flavala</i> Najer and Sychra, 2012 (in Najer et al., 2012)*†	1
<i>Hypsipetes leucocephalus</i>	Black bulbul	<i>Guimaraesiella</i> sp. 4	1
<i>Orthotomus sutorius</i>	Common tailorbird	<i>Philopteroides flavala</i> Najer and Sychra, 2012 (in Najer et al., 2012)*†	1
		<i>Menacanthus eurysternus</i> (Burmeister, 1838)†	5

Table II. Continued.

Bird species	Bird common name	Louse species	Louse no.
<i>Pomatorhinus gravivox</i>	Black-streaked scimitar babbler	<i>Resartor</i> sp. 1	15
<i>Pomatorhinus ruficollis</i>	Streak-breasted scimitar babbler	<i>Priceiella</i> sp. 1	82
<i>Stachyris nigriceps</i>	Grey-throated babbler	<i>Priceiella</i> sp. 2	1
<i>Stachyris striolata</i>	Spot-necked babbler	<i>Priceiella</i> sp. 3	5
<i>Stachyridopsis ruficeps</i>	Rufous-capped babbler	<i>Menacanthus eury sternus</i> (Burmeister, 1838)†	6
		<i>Myrsidea</i> sp. 4	3
<i>Macronus gularis</i>	Striped tit-babbler	<i>Guimaraesiella</i> sp. 5	2
<i>Alcippe dubia</i>	Rusty-capped fulvetta	<i>Myrsidea</i> sp. 5	2
<i>Alcippe davidi</i>	David's fulvetta	<i>Guimaraesiella</i> sp. 6	77
		<i>Myrsidea cheni</i> Price, Arnold and Bush 2006 (in Price et al., 2006) sensu lato	3
<i>Alcippe nipalensis</i>	Nepal fulvetta	<i>Guimaraesiella</i> sp. 6	16
		<i>Menacanthus</i> sp. (species unidentifiable)	1
		<i>Myrsidea</i> sp. 5	3
<i>Napothera brevicaudata</i>	Streaked wren-babbler	<i>Priceiella</i> sp. 4	57
<i>Pellorneum albiventre</i>	Spot-throated babbler	<i>Priceiella</i> sp. 4	3
<i>Pellorneum ruficeps</i>	Puff-throated babbler	<i>Priceiella</i> sp. 4	4
<i>Garrulax leucolophus</i>	White-crested laughingthrush	<i>Priceiella</i> sp. 5	3
<i>Garrulax maesi</i>	Grey laughingthrush	<i>Priceiella</i> sp. 5	9
		<i>Myrsidea</i> sp. 6	7
<i>Garrulax monileger</i>	Lesser necklaced laughingthrush	<i>Priceiella sternotypica</i> (Ansari, 1956) (in Gustafsson et al., 2018b) sensu lato	1
<i>Garrulax pectoralis</i>	Greater necklaced laughingthrush	<i>Priceiella sternotypica</i> (Ansari, 1956) (in Gustafsson et al., 2018b)	77
		<i>Menacanthus</i> sp. 1	2
		<i>Myrsidea orientalis</i> Tandan, 1972	17
<i>Garrulax chinensis</i>	Black-throated laughingthrush	<i>Priceiella</i> sp. 5	1
		<i>Myrsidea patkaiensis</i> Tandan, 1972*	3
<i>Garrulax caeruleus</i>	Grey-sided laughingthrush	<i>Priceiella</i> sp. 5	40
		<i>Myrsidea</i> sp. 7	18
<i>Minla cyanouoptera</i>	Blue-winged minla	<i>Resartor</i> sp. 2	2
		<i>Guimaraesiella</i> sp. 7	3
		<i>Myrsidea</i> sp. 8	1
<i>Minla ignotincta</i>	Red-tailed minla	<i>Resartor</i> sp. 3	10
		<i>Guimaraesiella</i> sp. 7	8
<i>Liocichla ripponi</i>	Scarlet-faced liocichla	<i>Myrsidea ananthakrishmani</i> Rai, 1978*	3
<i>Leiothrix lutea</i>	Red-billed leiothrix	<i>Guimaraesiella</i> sp. 8	25
<i>Heterophasia desgodinsi</i>	Black-headed sibia	<i>Resartor</i> sp. 4	7
		<i>Guimaraesiella</i> sp. 9	1
		<i>Myrsidea</i> sp. 9	1
<i>Lioparus chrysotis</i>	Golden-breasted fulvetta	<i>Resartor</i> sp. 5	8
		<i>Menacanthus eury sternus</i> (Burmeister, 1838)†	1
		<i>Myrsidea</i> sp. 10	16
<i>Suthora verreauxi</i>	Golden parrotbill	<i>Myrsidea</i> sp. 11	4
<i>Yuhina castaniceps</i>	Striated yuhina	<i>Turdinirmoides</i> sp. 1	1
<i>Yuhina flavicollis</i>	Whiskered yuhina	<i>Guimaraesiella</i> sp. 10	7
<i>Sitta nagaensis</i>	Chestnut-vented nuthatch	<i>Brueelia oxyrhyncha</i> Gustafsson, Chu, Bush and Zou, 2018 (in Gustafsson et al., 2018a)*†	4
<i>Geokichla citrina</i>	Orange-headed thrush	<i>Guimaraesiella</i> sp. 11	11
		<i>Myrsidea</i> sp. 12	13
		<i>Sturnidoecus</i> sp. 1	17
<i>Turdus hortulorum</i>	Grey-backed thrush	<i>Guimaraesiella</i> sp. 12	2
		<i>Myrsidea thoracica</i> (Giebel, 1874)*†	5
<i>Turdus dissimilis</i>	Black-breasted thrush	<i>Myrsidea thoracica</i> (Giebel, 1874)*†	3
		<i>Philopterus</i> sp. 3	1
<i>Turdus boulboul</i>	Grey-winged blackbird	<i>Myrsidea thoracica</i> (Giebel, 1874)*	8
<i>Tarsiger cyanurus</i>	Orange-flanked bluetail	<i>Menacanthus nogoma</i> Uchida, 1926*	2
<i>Copsychus saularis</i>	Oriental magpie robin	<i>Guimaraesiella</i> sp. 13	1
<i>Copsychus malabaricus</i>	White-rumped shama	<i>Guimaraesiella</i> sp. 13	3
		<i>Philopterus</i> sp. 4	4
<i>Enicurus leschenaulti</i>	White-crowned forktail	<i>Philopteroidea</i> sp. 1	2
<i>Cyornis unicolor</i>	Pale blue flycatcher	<i>Ricinus rubeculae</i> (Schrank, 1776)*†	10

Table II. Continued.

Bird species	Bird common name	Louse species	Louse no.
<i>Cyornis banyumas</i>	Hill blue flycatcher	<i>Guimaraesiella</i> sp. 13	3
<i>Cyornis concretus</i>	White-tailed flycatcher	<i>Myrsidea</i> sp. 13	4
<i>Anthipes monileger</i>	White-gorgeted flycatcher	<i>Guimaraesiella</i> sp. 13	2
		<i>Ricinus mugimaki</i> (Uchida, 1915)*†	2
<i>Niltava grandis</i>	Large niltava	<i>Menacanthus</i> sp. (species unidentifiable)	3
<i>Arachnothera magna</i>	Streaked spiderhunter	<i>Philopteroides</i> sp. 2	1
<i>Emberiza tristrami</i>	Tristram's bunting	<i>Brueelia</i> sp. 1	3
		<i>Menacanthus eurysternus</i> (Burmeister, 1838)†	5
Total		25 genera, 89 species	1005

* Chewing louse species are reported here for the first time from China.

† Lice on the following hosts all represent new host records.

differed among host families and species, we performed analysis of K independent sample nonparametric tests. Avian families were included in the analyses only if ≥ 5 individuals per species of at least 2 bird species were processed. Avian species were included in the analyses only if they occurred in 2 or more regions and included ≥ 5 individuals per region. In some bird orders, sample size was not large enough to make statistical analyses. We used a generalized linear mixed model (GLMM) to examine host diet and migratory status in relation to the prevalence of chewing lice. As fixed effects, we entered diet (3 categories: insectivorous, frugivorous, or omnivorous) and migratory status (2 categories: migratory or resident) as well as an interactive term (diet \times migratory) into the model. We used a normal distribution with identity link function, including host body mass as random effects, and we accounted for bird phylogeny by including a random hierarchical component in the model that consisted of a spatially nested term (genus within family) using the categorical code assigned to each unique taxon (Blackburn and Duncan, 2001). We ran a series of models, dropping those containing nonsignificant main effects and interactions, resulting in the best single model containing only significant terms. We analyzed increasingly restrictive datasets containing host species with at least 10 individual hosts sampled for lice (Sychra et al., 2011). Analyses were performed using SPSS 22 (IBM Corp., 2013) and are summarized in Table S1.

Ethical approval

This study was carried out in strict accordance with the guidelines of Regulations for the Administration of Laboratory Animals (Decree No. 2 of the State Science and Technology Commission of the People's Republic of China on 14 November 1988). We obtained approval for this study from the Guangdong Institute of Applied Biological Resources Administrative Panel on Laboratory Animal Care. Permission from the local forestry department was also obtained.

RESULTS

Louse species richness and abundance

In total, 2,210 birds, representing 215 species from 45 families, were searched for chewing lice. The sampled birds included 2,149 passerine birds spanning 194 species and 36 families and 61 nonpasserine birds belonging to 21 species in the orders Columbiformes, Galliformes, Coraciiformes, Strigiformes, Trogoniformes, and Piciformes. Lice were collected from 622 host

individuals (603 passerines belonging to 104 species and 19 nonpasserines belonging to 13 species), giving an overall prevalence of 28.1%. In total, 5,251 chewing lice were collected from 622 birds. Table S1 lists all host species and numbers of hosts sampled for lice, together with data on parasitological parameters, as well as the values for host variables that were significantly correlated with louse prevalence.

In total, 1,005 chewing louse specimens were slide mounted and identified from 186 bird individuals. The lice collected belong to 89 species, 25 genera, and 3 families in 2 suborders (Amblycera and Ischnocera), as shown in Table II.

Differences of louse prevalence and intensity among birds

Infestation rates were the highest in the Columbiformes and Galliformes (100%), followed by Coraciiformes (75.0%), Cuculiformes (61.5%), Strigiformes (28.6%), Passeriformes (28.1%), Trogoniformes (27.3%), and Piciformes (16.1%), respectively.

Among host families, the prevalence (mean \pm SE) of chewing lice varied significantly ($\chi^2 = 38.096$, $df = 16$, $P = 0.001$; Fig. 2),

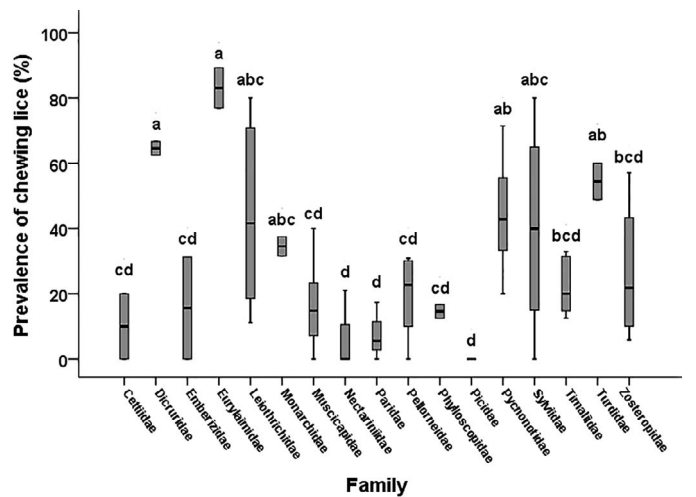


Figure 2. Prevalence of chewing louse infestations from selected species within some avian host families from southern China. Avian families were included in this analysis only if they had 2 or more bird species with ≥ 5 individuals deloused per species. There was a significant difference among avian host families ($\chi^2 = 38.096$, $df = 16$, $P = 0.001$). Different letters indicate significant differences for $P < 0.05$. The error bars represent SEs of the means.

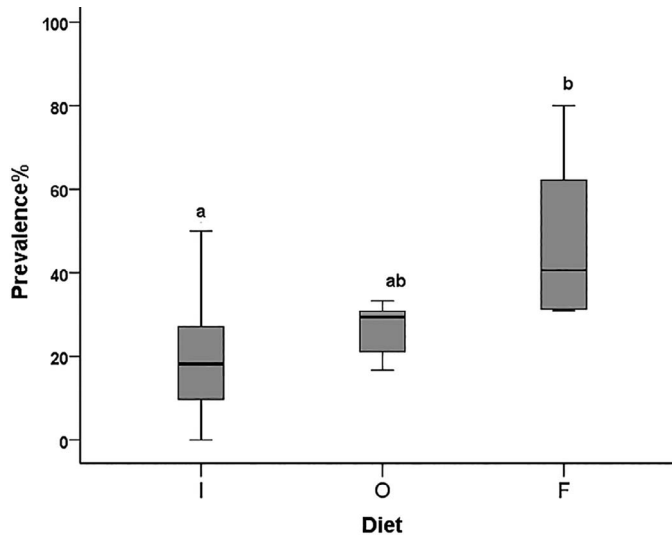


Figure 3. Prevalence of chewing louse infestations in relation to different host food guilds. Bird species were included in this analysis only if 10 or more individuals were deloused. I, insectivorous birds; F, frugivorous birds; O, omnivorous birds. Different letters indicate significant differences for $P < 0.05$; The error bars represent SEs of the means.

ranging from 0% in Picidae to $83.1 \pm 6.2\%$ in Eurylaimidae. Among the Passeriformes, the chewing lice prevalence varied significantly among species ($\chi^2 = 47.274$, $df = 29$, $P = 0.017$), with the silver-breasted broadbill (*Serilophus lunatus*) having the highest prevalence ($97.2 \pm 2.8\%$).

The mean abundance and mean intensity of all the chewing lice collected was 2.4 and 8.4, respectively (range, 0–340). The mean abundance ($\chi^2 = 10.9$, $df = 11$, $P < 0.001$) and mean intensity ($\chi^2 = 29.8$, $df = 11$, $P = 0.002$) were significantly different among bird species, with the silver-breasted broadbill (7.5 ± 1.9) having the highest mean abundance and the orange-headed thrush (*Geokichla citrina*) (10.8 ± 3.3) having the highest mean intensity (Table S1).

Differences of louse prevalence among climatic zones, host diet, and migratory status

We compared the louse prevalence among climatic zones but found no significant differences ($\chi^2 = 5.940$, $df = 3$, $P = 0.115$). The results of the GLMM generated a significant model for prevalence ($F_{5,48} = 4.635$, $P = 0.002$) but only included a diet as a predictor ($P = 0.001$). Insectivorous birds had the lowest prevalence ($21.6 \pm 3.3\%$; Fig. 3). There was no significant difference between migratory and resident species (Mann–Whitney U-test, $U = 203.00$, $P = 0.128$). Resident birds had a higher prevalence of chewing lice (21.4 ± 3.3 vs. 17.9 ± 4.3 for migratory birds).

Relationship between louse prevalence or intensity and host morphology

Spearman correlation analyses were restricted to bird species with at least 10 individuals sampled, and they showed that prevalence is positively correlated with host body mass ($r = 0.356$, $P = 0.008$) and bill length ($r = 0.310$, $P = 0.022$). Mean intensity was also positively correlated with host body mass ($r = 0.292$, $P =$

0.032). In contrast, bill length was not correlated with louse intensity ($r = 0.193$, $P = 0.162$; Fig. 4).

DISCUSSION

Comparative studies of parasite community ecology are often hampered by uneven data sets merged from a number of smaller studies by researchers using different methods. We used consistent methodology to compare parasite prevalence and intensity across a diverse set of bird species sampled in southern China. Sampling a diverse set of host species is desirable because it increases the range of variation in host parameters that, in turn, increases the inferential power of a comparative study.

In this study, louse samples were identified to species where possible and identified as morphospecies when full identifications could not be made (Table II). Among the 89 morphospecies, 9 species were previously recorded from China by Huang (2003), Hellenthal and Price (2003), and Price et al. (2006). Here, we report 28 species for the first time from China; the other 52 species are only identified to genus. Note that as the published list of Huang (2003) is of dubious authenticity, the true number of new records for China is likely higher than shown here. New host records of chewing lice recorded in this study are indicated in Table II.

The total prevalence of chewing lice in this study was 28.1%. This infestation rate is lower than those recorded in similar surveys, such as Dik et al. (2011a), Inci et al. (2010), and Wheeler and Threlfall (1986), with 35.48, 41.4, and 41% of birds parasitized, respectively. The discrepancy between our results and those obtained in these 3 reports could be due to differences in methodological and sampling methods. In our study, chewing lice were collected by visual examination and a fumigation chamber with visual search of the head of live birds, unlike the other studies in which birds were killed for sampling.

However, another survey by Dik et al. (2011b) of lice from Passeriformes showed an even lower infestation rate than our rate, with 21.57% of birds infested. The similarity of these low infestation rates is likely due to Passeriformes frequently showing low prevalence (e.g., Palma and Price, 2010) and, in our study, most of the bird species belong to this order of birds. On the species level, we found that the prevalence of chewing lice in Eurylaimidae was the highest among all families, with an average of 83.1%. This finding is consistent with a previous study that showed that 32 black-and-red broadbills (*Cymbirhynchus macrorhynchos*; Eurylaimidae) examined for chewing lice in Vietnam had a prevalence of 100% (Sychra et al., 2014).

Bird species, and especially bird families, vary greatly in morphology. Host body mass is known to have an influence on the abundance of parasites and other parameters (Clayton and Walther, 2001). Previous studies have demonstrated significant correlations between parasite species richness and host body size, local population density, and geographic range size (e.g., Rózsa, 1997). Louse populations on avian hosts range from none to thousands per host (Marshall, 1981). In the present study, there was a positive correlation between host body mass and mean intensity. Previous studies showed a similar correlation between host body size and abundance in a group of parasites (Poulin and Rohde, 1997; Grutter and Poulin, 1998). Rózsa (1997) showed a correlation between host body mass and mean abundance of lice among 36 species of birds from temperate climate; he hypothe-

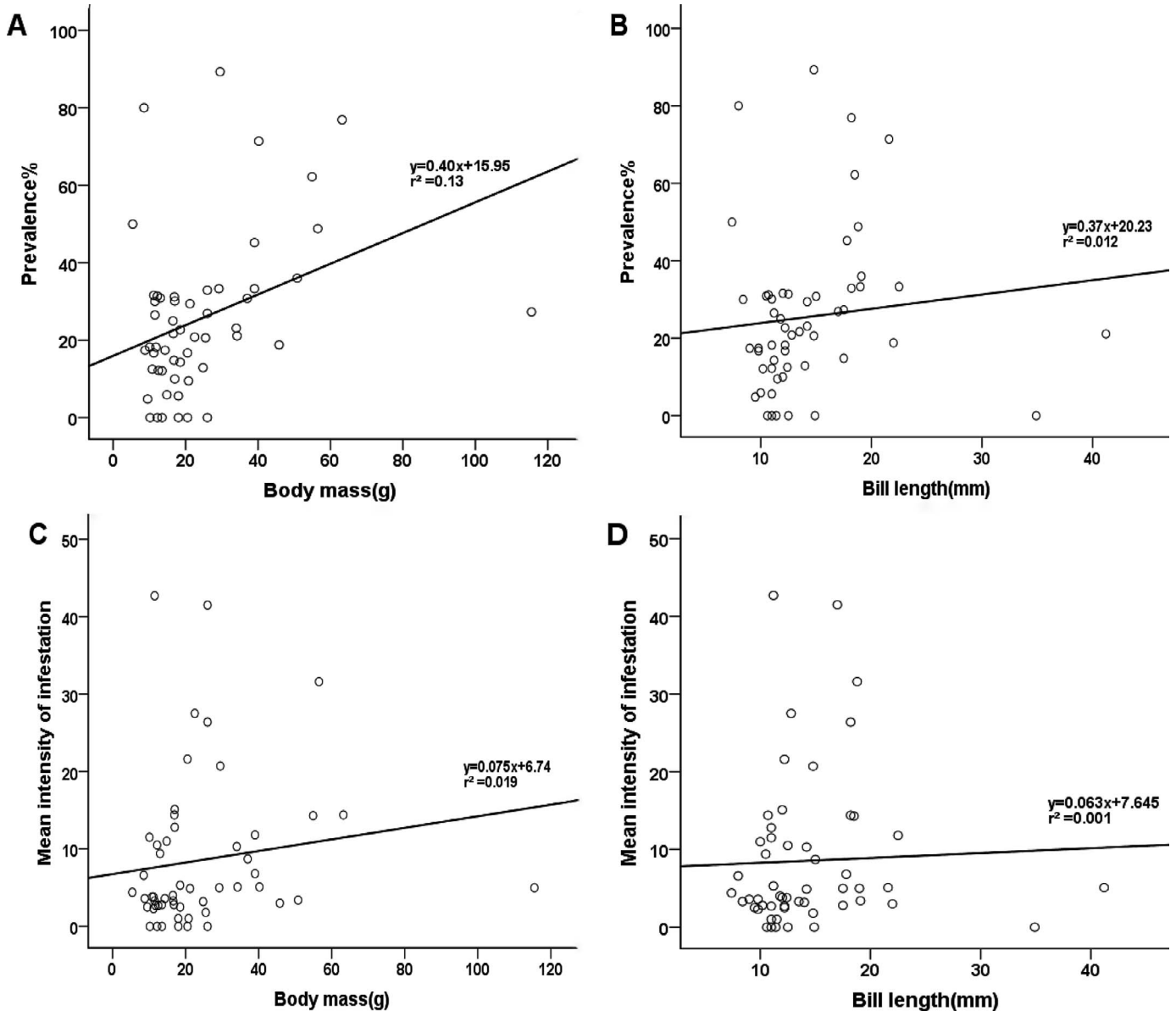


Figure 4. Prevalence of chewing lice from different bird species in relation to (A) mean host body mass and (B) mean host bill length. Mean intensity of chewing lice from different bird species in relation to (C) mean host body mass and (D) mean host bill length. Bird species were included in this analysis only if 10 or more individuals were deloused.

sized that the correlation could be explained by (1) more resources on larger hosts; (2) more refugia from preening on larger hosts; or (3) greater longevity of larger hosts, thereby provide a larger window of opportunity for infestation by lice. Our data are insufficient to evaluate the relative merits of these hypotheses. Further comparative and experimental studies should be made to test these possible explanations.

We found louse prevalence to be positively correlated with host bill length, whereas mean intensity was not significantly correlated with host bill length (Fig. 4). Bills are important tools for preening, a major defense against ectoparasites. Efficient preening reduces the number of lice, and, consequently, the feather damage that they cause. Inefficient preening results in a rapid increase in ectoparasite load (Brown, 1972, 1974; Clayton, 1991). Preening

efficiency may vary with bill size. Indeed, Barbosa (1996) pointed out long-billed species spend more time preening during bouts of foraging than short-billed species, suggesting that species with long bills might be less efficient at preening than birds with short bills. Wild birds with beak deformities have been shown to have heavier louse infestations than birds without beak deformities (Worth, 1940; Johnson and Long, 1959).

Beak morphology is usually interpreted in relation to its critical role in feeding (Clayton et al., 2005). Beak types vary in shape because of the different ways birds collect food. In particular, the bill overhang is known to be important to combat louse infestations (Clayton et al., 2010), and even a small difference in overhang size may have a dramatic effect on louse load (Clayton et al., 2005); however, this effect is apparently absent in

nonpasserines (Clayton and Walther, 2001). Differences in feeding method may thus influence the shape of the beak that, in turn, influences the bird's efficiency in removing ectoparasites. Given the importance of the bill shape for removing lice in passeriform birds, as well as for feeding, we would expect differences in louse loads to vary between guilds of birds that have consistent differences in bill shape, particularly for the degree of bill overhang.

Our data indicate that chewing louse infestation rates were affected by host food guild, with prevalence being lower on insectivorous birds than on frugivorous and omnivorous birds. However, data on the degree of bill overhang were not collected, and we are thus presently unable to test whether this character can explain the pattern our data indicate. In general, we would expect an insectivorous bird to have more use of a bill overhang in food manipulation than a frugivorous bird, as the prey item of an insectivorous bird would struggle more than that of a frugivorous bird. By contrast, bill overhang could even be a hindrance in frugivorous or granivorous birds if it prevents the bird from properly manipulating food (Clayton and Walther, 2001). However, additional data on the degree of bill overhang in the 3 food guilds examined are needed to test this hypothesis.

The 4 climatic zones where we collected lice differed in relative temperature and humidity, but there were no significant differences in the prevalence of chewing lice among the zones. This is in agreement with the finding of Tolossa et al. (2009) but in contrast to the data of Moyer et al. (2002a). In the present data, the lack of difference in louse prevalence between the different climatic zones may be due to the relatively similar climates in the 4 zones.

Migratory animals differ from resident forms by being exposed to more than a single environment and its predators, parasites, and other biotic components. Some studies of protozoan parasites in birds suggest that migratory species have more severe infections than residents (Bennett and Fallis, 1960; Greiner et al., 1975). The energy cost of migration is very high for birds, and more time is therefore needed for feeding, at the cost of other activities, including preening. This may result in an increase in chewing lice abundance in migratory birds (Rózsa, 1997; Price et al., 2003).

However, in this study we found no difference in louse prevalence between migratory and resident birds. This is surprising, as migratory birds at higher latitudes generally have much lower louse infestation rates than resident birds (D. R. Gustafsson, unpubl. data from Sweden and Japan). Sychra et al. (2011) also showed a significant difference in the total prevalence of chewing lice on resident and migratory birds. The differences between our data and data from outside China are hard to explain. However, many of the species here counted as migratory breeds in southern China and migrate to, for example, Southeast Asia. This means that in contrast to the birds examined by Sychra et al. (2011), many of the specific individuals of these bird species we examined would still have bred in the subtropical area. Their louse communities would therefore have been influenced more by conditions prevailing in the subtropics than in the temperate or boreal regions, where the birds examined by Sychra et al. (2011) and D. R. Gustafsson (unpubl. data) would have bred. Differences in louse communities over such large scales are very poorly known, and future work will focus on comparing the louse loads of birds breeding in the temperate and subtropical regions, including both migrants and nonmigrants.

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