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What are the factors determining the probability of discovering a flea species (Siphonaptera)?

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Abstract Our aim was to determine which of four variables (number of host species exploited by the parasite, taxonomic distinctness of these hosts, geographic range of the principal host, and year of description of this host) was the best predictor of description date of fleas. The study used previously published data on 297 flea species parasitic on 197 species of small mammals from 34 different regions of the Holarctic and one region from the Neotropics. We used both simple linear and multiple regressions to evaluate the relationships between the four predictor variables and the year of flea description, on species values as well as on phylogenetically independent contrasts. Whether or not the analyses controlled for flea phylogeny, all predictor variables correlated significantly with year of flea description when tested separately. In multiple regressions, however, the number of exploited host species was the best predictor of the date of flea description, with the geographic range of the principal host species as well as the date of its description having a lesser, though significant, influence. Overall, our results indicate that a flea species is more likely to be discovered and described early if its biological characteristics (exploitation of many host species) and those of its hosts (long-known to science, broad geographic distributions) increase its chances of being included in a collection. Because the variables we investigated only explained about 10–11% of the variation in year of description among flea species, other factors must be important, such as temporal variability in the activity of flea taxonomists.

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Introduction

Discovery and scientific description of new species of plants and animals is an on-going process that, in its modern form, dates back to the pioneering approach of Linnaeus. In spite of continuing efforts by zoologists and botanists, the inventory of existing species is far from being complete, and the number of discovered species is evaluated at only 15–18% of the entire number of extant species (Heywood and Watson 1995; Wilson 2003). The rate of discovery of new species not only differs sharply among different taxa for various reasons, but also can greatly fluctuate on a temporal scale within a taxon. For example, some species have been described much later than their close relatives. In other words, the probability of a species being discovered can be profoundly different among species of the same taxon (Gaston 1991; Gaston and Blackburn 1994; Collen et al. 2004).

Recent studies have showed that the probability of a species being discovered, although involving an element of chance, is strongly affected by the biological characteristics of that species (e.g., Gaston 1991; Medellin and Soberon 1999; Cabrero-Sanudo and Lobo 2003). In fact, Collen et al. (2004) listed as many as six different (not necessarily exclusive) hypotheses about the correlates of the probability of a species being discovered. According to these hypotheses, the date of description of a species is influenced by some of its biological attributes, the main ones being body size, geographic range, geographic location and density. However, most of these hypotheses have been tested using a very limited range of taxa, mainly birds (e.g., Gaston and Blackburn 1994), some mammalian orders (e.g., Collen et al. 2004), butterflies (e.g., Gaston et al. 1995) and beetles (Cabrero-Sanudo and Lobo 2003). The results of these studies indicate that different biological correlates of description date apply to different taxa. Nevertheless, a correlation between description date and some biological parameters appeared to be almost universal. For example, geographic range was found to be a good predictor of the date of species discovery across various taxa (Gaston et al. 1995; Blackburn and Gaston 1995; Allsop 1997; Collen et al. 2004). In other words, species with larger geographical ranges are more likely to be encountered early by collectors compared with species with limited geographic distributions.

The link between biological parameters of species and their probability of discovery has been shown to exist not only for free-living animals but also for parasites. Indeed, different probabilities of discovery among parasite species of various taxa have been shown to be associated with their body size (Poulin 1996, 2002). In copepods parasitic on fish hosts, Poulin (1996) found a negative correlation between parasite body size and year of description. Poulin (2002) showed that the monogenean species currently being described are smaller than those previously known. However, the relationships between the date of discovery and any biological parameters other than body size have never been studied in any parasite taxon.

The ubiquitous negative relationship between geographic range and the year of species discovery found in free-living animals can be also true for parasites. Furthermore, in this context, an equivalent to the geographical range of a free-living species in a parasite species may be the extent of its host range (measured as the number of host species used). If free-living animals with larger geographical ranges are more likely to be encountered first, then parasite species exploiting a larger number of host species may also be more likely to be encountered and described early than more host-specific parasite species. Beyond the number of host species we might expect the phylogenetic or taxonomic relatedness of host species to matter. If niche conservatism occurs (Peterson et al. 1999; Webb and Gaston 2003), i.e. if related species share functional or ecological attributes, we can hypothesize that parasite species exploiting closely related hosts are less likely to be discovered than parasite species exploiting totally unrelated host species which have different ecological requirements, body size or behavior. Thus, for a given number of exploited hosts we might expect that a parasite infesting a higher taxonomic diversity of hosts should be discovered before one infesting closely related hosts.

Poulin (1996) reported that, although a correlation between copepod body size and the date of description existed for species parasitic on fish hosts, there was no relationship between these variables among copepods parasitic on invertebrate hosts. For monogeneans, it was noted that species infecting tropical or deep-water fish are most likely not as well surveyed as those of temperate fish or commercially important fish species (Poulin 2002). This means that the probability of a parasite species being discovered depends not only on some attributes of this species, but also on some attributes of its hosts. The latter is true because it is the host species that is primarily sampled in the field, whereas sampling of most parasites is only a secondary process following to host sampling. For example, a parasite species exploiting a widely distributed host species is likely to be found earlier than a similar species on a host with smaller geographic range.

Here, we used published data on fleas (Siphonaptera) parasitic on small mammals from 35 distinct geographic regions and examined the relationships between the year of a flea species discovery and its degree of host specificity as well as the geographic range and year of description of its principal host species. Fleas are holometabolous insect parasites of higher vertebrates, being most abundant and diverse on small mammals. In addition to using the number of host species used by a flea as a measure of host specificity, we also applied a measure of host specificity that takes into account the taxonomic or phylogenetic affinities of the various host species (Poulin and Mouillot 2003). This measure emphasizes the taxonomic distance between host species used by a flea rather than their number, providing a different perspective on host specificity, one that truly focuses on the specialization of the flea for its host habitat.

Materials and methods

Data set

Data were obtained from published surveys that reported flea distribution and abundance on small mammals (Didelphimorphia, Insectivora, Lagomorpha and Rodentia) in 35 different regions (Table 1). These sources provided data on the number of individuals of each flea species found on a given number of individuals of each particular host species, except for the Barguzin depression for which data on the average abundance of a flea species on a host species were provided instead (Vershinina et al. 1967). Single findings of a flea species on a host species or in a region were considered accidental and were not included in the analysis. In total, we used data on 838 flea species-region combinations, which included 297 flea species found on 197 mammalian species.

For each flea species, two measures of host specificity were used: (1) the number of mammalian species on which the flea species was found, and (2) the specificity index, S_{TD}, and its variance $VarS_{\mathrm{TD}}$ (Poulin and

Table 1 Data on number of species of small mammals and fleas from the 35 regions used in the analyses

Region	Number of species		Source
	Hosts	Fleas	
Southeastern Brazil	16	10	de Moraes et al. (2003)
Idaho	15	31	Allred (1968)
Central California	19	22	Linsdale and Davis (1956)
Southwestern California	9	17	Davis et al. (2002)
Northern New Mexico	29	34	Morlan (1955)
Slovakia	20	22	Stanko et al. (2002)
Volga-Kama region, Russia	20	31	Nazarova (1981)
Novosibirsk region, southern Siberia	19	28	Violovich (1969)
Altai mountains, Russia	24	10	Sapegina et al. (1981)
Western Sayan ridge, southern Siberia	15	29	Emelyanova and Shtilmark (1967)
Tuva, Russia	13	28	Letov et al. (1966)
Selenga region, central Siberia	9	13	Pauller et al. (1966)
Barguzin depression, Baikal rift zone	17	29	Vershinina et al. (1967)
Central Yakutia, Russia	6	17	Elshanskaya and Popov (1972)
Amur river valley, southern Russian Far East	9	22	Koshkin (1966)
Ussury river valley, southern Russian Far East	9	21	Kozlovskaya (1958)
Khasan lake region, southernmost Russian Far East	9	12	Leonov (1958)
Magadan and Tchukotka region, northern Russian Asian Far East	15	16	Yudin et al. (1976)
Kamchatka peninsula, eastern Russian Far East	4	8	Paramonov et al. (1966)
Kabarda, northern Caucasus	9	21	Syrvacheva (1964)
Adzharia, southern Caucasus	12	20	Alania et al. (1964)
Southwestern Azerbaijan	14	23	Kunitsky and Kunitskaya (1962)
Turkmenistan	18	42	Zagniborodova (1960)
Kustanai region, northwestern Kazakhstan	17	19	Reshetnikova (1959)
Akmolinsk region, northern Kazakhstan	19	26	Mikulin (1959a)
Pavlodar region, eastern Kazakhstan	16	14	Sineltschikov (1956)
Moyynkum desert, southern Kazakhstan	18	32	Popova (1968)
East Balkhash desert, Kazakhstan	22	39	Mikulin (1959b)
Dzhungarskyi Alatau ridge, Kazakhstan	15	23	Burdelova (1996)
Tarbagatai ridge, eastern Kazakhstan	23	37	Mikulin (1958)
Kyrgyz ridge, northern Kyrgyzstan	16	36	Shwartz et al. (1958)
Gissar ridge, Tajikistan	8	25	Morozkina et al. (1971)
Northwestern Khangay region, Mongolia	21	44	Labunets (1967)
Central Khangay region, Mongolia	9	23	Vasiliev (1966)
Negev desert, Israel	13	11	Krasnov et al. (1997 and unpublished data)

Mouillot 2003). The index S_{TD} measures the average taxonomic distinctness of all host species used by a parasite species. When these host species are placed within a taxonomic hierarchy, the average taxonomic distinctness is simply the mean number of steps up the hierarchy that must be taken to reach a taxon common to two host species, computed across all possible pairs of host species (see Poulin and Mouillot 2003, for details). The greater the taxonomic distinctness between host species, the higher the value of the index S_{TD}: thus, it is actually inversely proportional to specificity. A high index value means that on average the hosts of a flea species are not closely related. Using the taxonomic classification of Wilson and Reeder (1993), all mammal species included here were fitted into a taxonomic structure with five hierarchical levels above species, i.e. genus, subfamily, family, order and class (Mammalia). The maximum value that the index S_{TD} can take (when all host species belong to different orders) is thus 5, and its lowest value (when all host species are congeners) is 1. However, since the index cannot be computed for parasites exploiting a single host species, we assigned a S_{TD} value of 0 to these flea species, to reflect their strict host specificity. The variance in S_{TD}, $VarS_{TD}$, provides information on any asymmetries in the taxonomic distribution of host species (Poulin and Mouillot 2003); it can only be computed when a parasite exploits three or more host species (it always equals zero with two host species). To calculate S_{TD} and $VarS_{TD}$, DM and RP developed a computer program using Borland C++ Builder 6.0 (available at http://www.otago.ac.nz/zoology/downloads/poulin/TaxoBiodiv1.2).

Measures of host specificity were averaged across regions for each flea species that occurred in more than one region. In addition, the number of host individuals examined was weakly, albeit significantly correlated with the number of host species ($r^2 = 0.03$, $F_{1,\ 295} = 8.2$, $P < 0.005$), but not with either S_{TD} or $VarS_{TD}$ ($r^2 = 0.01$, $F_{1,\ 295} = 3.6$ and $r^2 = 0.0005$, $F_{1,\ 295} = 0.2$, respectively; $P > 0.05$ for both). To avoid the potential confounding effects of host sampling effort, the residuals of the regression of the log-transformed number of host species on which the flea species was found against the log-transformed number of host individuals sampled were used in subsequent analyses.

Description dates for fleas were taken from the catalog of the Rothschild collection of fleas (Hopkins and Rothschild 1953, 1956, 1962, 1966, 1971; Traub et al. 1983; Smit 1987) and from the Interactive Flea Taxonomic Database compiled by Medvedev and Lobanov (1999; available at http://www.zin.ru/Animalia/Siphonaptera/taxfind2.htm).

We calculated the mean abundance (mean number of fleas per sampled host) of each flea species on each host species in each region. Other measurements of infection level, such as prevalence and intensity of flea infestation, were not available for the majority of the regions considered. Then, we identified the principal host for each flea species across all regions, i.e. the mammal species in which the flea attained its highest abundance. For each of these host species, the geographic range and date of description were obtained. Geographic ranges were generated from distribution maps of each host species. Distribution range maps were composed as polygon maps using the ArcView 3.2 software based on maps from various sources (see Krasnov et al. 2004 for details). Synanthropous widespread species (*Mus musculus*,*Rattus rattus* and *Rattus norvegicus*) were considered in the borders of their natural geographic ranges only. Host description dates were taken from Wilson and Reeder (1993). Across host species, host description date was significantly negatively correlated with the size of the host geographic range ($r^2 = 0.44$, $F_{1,\ 295} = 232.9$, $P < 0.005$). Consequently, the original values of the host description dates were substituted by values of their residuals from the regression of the log-transformed host description dates against the log-transformed area of the host geographic ranges.

Data analysis

All variables were logarithmically transformed prior to analyses to equalize variances. To examine if the degree of host specificity and/or host geographic range and host date of description are associated with the probability of flea discovery we examined the relationship between the date of description of a flea species and measures of its host specificity (number of exploited host species, their taxonomic distinctness and asymmetry) and two parameters of its principal host (geographic range and date of description) using both separate (linear) and multiple (forward stepwise) regressions.

Treating species as statistically independent data points in a comparative study may be invalid as it can introduce bias in the analysis (Harvey and Pagel 1991). To control for the effects of flea phylogeny, we used the method of independent contrasts (Felsenstein 1985; Pagel 1992). The phylogenetic tree for fleas was based on the taxonomy used in Hopkins and Rothschild (1953, 1956, 1962, 1966, 1971), Smit (1987) and Traub et al. (1983) and the cladistic tree of flea families of Medvedev (1998). To compute independent contrasts, we used the PDAP:PDTREE module (Garland et al. 1993; Midford et al. 2003) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison and Maddison 2004). Independent contrasts were standardized as suggested by Garland et al. (1992). To examine the relationships of description and predictor variables using independent contrasts, we used both separate and multiple (forward stepwise) major axis regressions forced through the origin (Pagel 1992; Garland et al. 1993).

Results

The earliest description of a flea species from our data set dates back to 1800, whereas the latest description

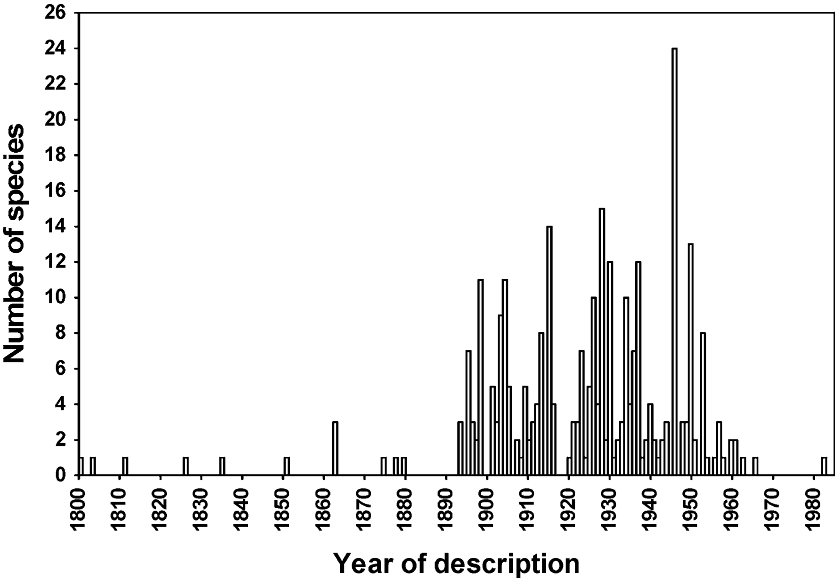

Fig. 1 Frequency distribution of dates of description for 297 flea species

Table 2 Summary of conventional and independent contrasts separate regression analyses of date of species description versus flea and host parameters for 297 flea species

Predictor	Intercept	Slope	r^2	F	P
Conventional					
Number of host species	7.56	−0.004	0.03	10.5	0.001
S_{TD}	7.56	−0.004	0.03	8.3	0.004
$VarS_{\mathrm{TD}}$	7.56	−0.004	0.01	4.4	0.03
Host geographic range	7.57	−0.002	0.06	19.2	0.001
Date of description of the principal host	7.56	0.09	0.02	6.2	0.01
Independent contrasts					
Predictor			r	F	p
Number of host species			−0.26	21.9	0.00001
S_{TD}			−0.22	15.2	0.0001
$VarS_{\mathrm{TD}}$			−0.13	5.1	0.02
Host geographic range			−0.17	8.6	0.003
Date of description of the principal host			0.12	4.7	0.03

occurred in 1983 (Fig.1). The frequency distribution of dates of description in fleas demonstrates that the vast majority of flea species was discovered from the beginning to the middle of the last century. In addition, periods when many flea species have been described alternated with periods when the rate of flea descriptions was extremely low (even reaching zero per year).

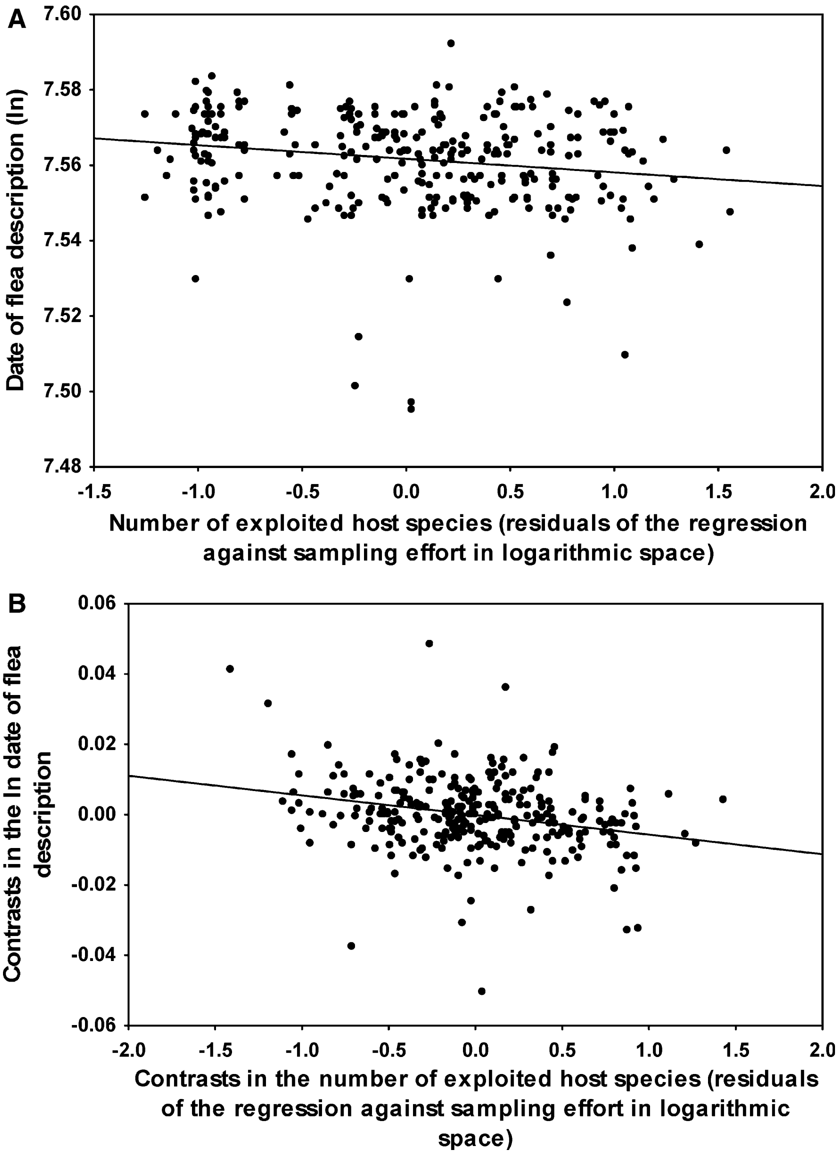

Fig. 2 Relationship between the date of description and the number of host species among 297 flea species (**a** conventional data points, **b** independent contrasts)

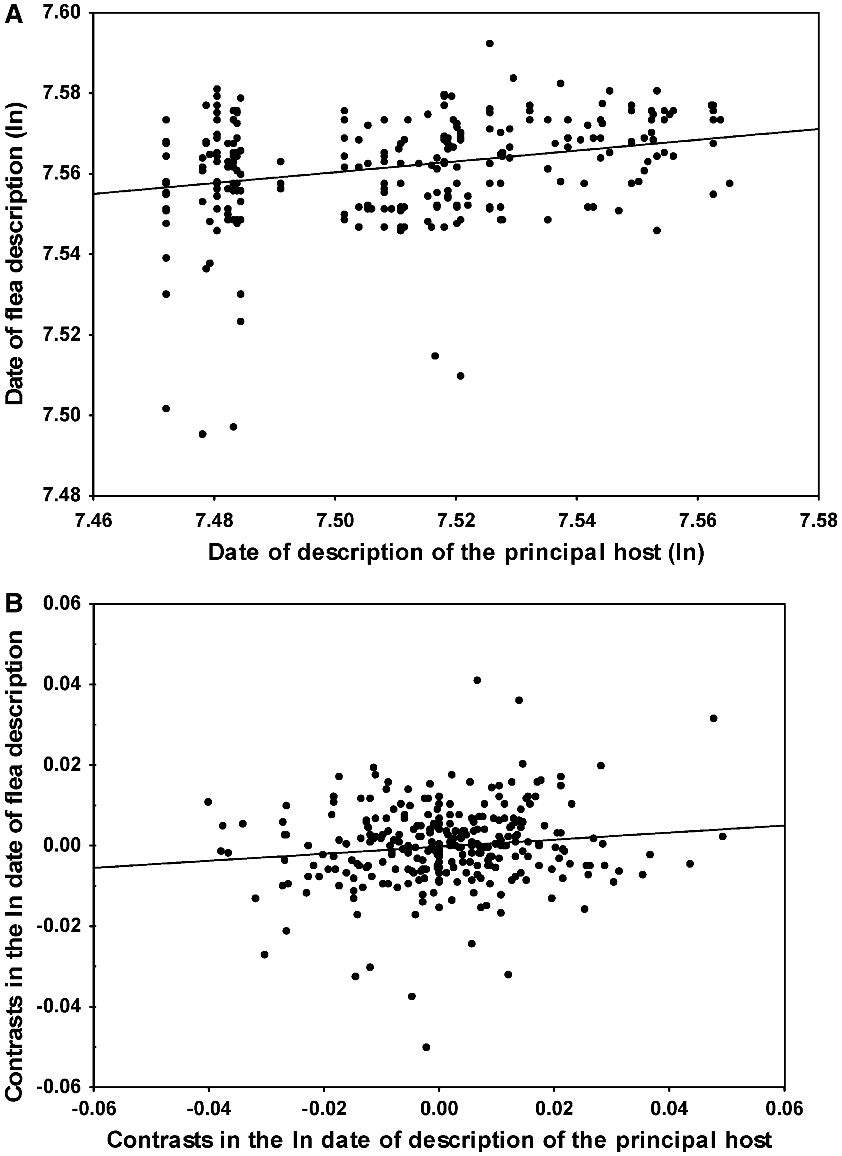

Fig. 3 Relationship between the date of flea description and the date of description of the principal host species among 297 flea species (**a** conventional data points, **b** independent contrasts)

Separate analyses (linear regressions) of the relationships between the date of flea description and measures of host specificity demonstrated that the date of flea description was weakly, albeit significantly negatively correlated with each of the host specificity measure (Table 2; Fig.2a for the number of exploited hosts). The same was true for the relationship between the date of flea description and the geographic range of the principal host species (Table 2). In contrast, the date of flea description was weakly positively correlated with the date of description of the principal host (Table 2; Fig.3a). Separate analyses using independent contrasts provided essentially the same results (Table 2; Figs.2b, 3b).

Multiple regression models using both conventional data and independent contrasts demonstrated that the number of exploited host species was the best predictor of the date of flea description, whereas the predicting power of the geographic range of the principal host species as well as the date of its description was lower, albeit significant (Table 3). However, multiple models explained only 10% (conventional analysis) and 11% (independent contrasts analysis) of the total variance.

Discussion

Our results demonstrate that the probability of a flea species being discovered and described is determined mainly by its degree of host specificity. In general, fleas that exploit larger number of host species are discovered earlier than more host-specific fleas. The likelihood of discovery is also higher for the flea species that parasitize hosts with larger geographic range. In addition, the earlier a host species becomes known to science, the earlier its parasites are described.

The mechanism behind this is obvious. The probability of a flea being encountered by a collector is higher when this flea occurs on a higher number of host species.

Table 3 Multiple regressions of conventional data and independent contrasts predicting the date of discovery for 297 flea species

Predictor	Intercept	Slope	t	P
Conventional data ($r^2 = 0.10$, $F_{3,\ 293} = 11.4$, $P < 0.001$)				
Number of host species	7.57	−0.002	−3.91	0.0001
Host geographic range		−0.003	−2.77	0.005
Date of description of the principal host		0.1	2.75	0.006
Predictor		Slope	t	P
Independent contrasts ($r = 0.34$, $F_{3,\ 293} = 9.55$, $P < 0.001$)				
Number of host species		−0.007	−4.26	0.00003
Host geographic range		−0.001	−2.58	0.01
Date of description of the principal host		0.10	2.87	0.004

The reason for this is that, in field surveys, the primary targets are, usually, hosts rather than parasites. Consequently, a survey of parasites results from a survey of hosts. The correlation between flea description date and geographic range and description date of its principal host species supports the idea that the discovery of a parasite species is somewhat secondary to the discovery of a host species. The probability of the latter being found, in turn, is to a large degree determined by its geographic range. This was found to be true for various animal taxa such as beetles (Allsop 1997), butterflies (Gaston et al. 1995), passerine birds (Blackburn and Gaston 1995), carnivores and primates (Collen et al. 2004, for both). This was also supported by a secondary result of this study that showed a negative correlation between the geographic range and year of description of small mammals.

Both conventional analyses and analyses using independent contrasts provided roughly the same results. This suggests the absence of a phylogenetic effect on the relationships between the date of flea discovery and the biological parameters investigated here. Indeed, the dependent variable in this study (the year in which a species has been described) measures, in fact, the efficiency of humans at finding parasite species. This efficiency proved not to be influenced by flea phylogeny, although phylogeny appears to matter for other animal taxa (e.g., Collen et al. 2004).

Different measures of flea host specificity were found to have different predictive power in relation to the flea description date, with the number of exploited host species having the highest predictive power followed by S_{TD} and $VarS_{\mathrm{TD}}$. Significant correlations between the date of flea description and these two measures of host specificity were only found using separate regression analyses and subsequently disappeared when multiple regressions were used. This indicates that each of these measures explains only a small fraction of the total variance in the date of flea description. In other words, the number of host species exploited by a flea species is much more important than the taxonomic composition of these hosts from the perspective of the probability of this flea being found by a collector. Still, the relationship between S_{TD} and the date of flea description estimated by a linear regression is quite clear, especially when based on independent contrasts ($r = -0.22$, $P = 0.0001$). This suggests that flea species exploiting a broad taxonomic range of hosts are more likely to be discovered early than fleas exploiting only closely related species. Assuming that closely related mammals have common ecological attributes due to niche conservatism (Martinez-Meyer et al. 2004), we suspect that the diversity of host ecological attributes increases the diversity of ways in which their fleas can be discovered. For instance mammalian body size is highly conserved across the taxonomic hierarchy (Smith et al. 2004). Flea species infesting hosts with a large range of body size have a higher likelihood of being discovered because this diversity of body sizes increases the number of ways in which a mammal may be sampled: poisoning, trapping or hunting efficiency are certainly related to particular size ranges. For example, *Ctenophthalmus breviatus* that exploit hosts of four rodent and one insectivore families ranging in body size from 8000 g (*Marmota bobac*) to 8 g (*Sorex araneus*) was described in 1926, whereas *Ctenophthalmus shovi* parasitizing hosts of two rodent and one insectivore families ranging in body size from 40 g (*Apodemus mystacinus*) to 8 g (*Sorex satunini*) was discovered in 1948.

In spite of a significant correlation between the date of flea discovery and some of the independent variables used in this study (the number of exploited host species and the geographic range and date of description of the principal host species), the proportion of the total variance explained by these variables was low. This suggests that there are other key determinants of the probability of a flea being found and described. For example, larger species have been discovered earlier than smaller species in some animal taxa (e.g., Gaston and Blackburn 1994 for birds; Cabrero-Sanudo and Lobo 2003 for dung beetles), including parasites (e.g., Poulin 1996 for copepods parasitic on fish hosts; Poulin 2002 for monogeneans). In contrast, body size was a poor predictor of the description dates in other taxa (e.g., Allsop 1997 for scarab beetles; Collen et al. 2004 for primates). In parasite groups where a relationship between body size and year of description has been shown, body sizes vary by a few orders of magnitude (Poulin 1996, 2002). This variation is much lower among the flea species considered (the body length of the smaller species in our dataset are about 1.5–2 mm, whereas, that of the larger species is about 2.8–3.8 mm), so it is unlikely to greatly affect whether a flea is seen or whether it goes unnoticed by a collector.

The low proportion of the total variance explained by the biological parameters used in this study can be caused by a ''human factor'' in the history of flea taxonomy. Indeed, the apparent peaks in the frequency distribution of flea description dates (Fig. 1) suggest that periods of intense description and publication activity by one or more key taxonomists working on fleas have alternated with periods when few or no new flea species were described. For example, the three highest peaks on Fig.1 coincide with the clustered descriptions of multiple new flea species by highly productive taxonomists such as Rothschild (1915a, b), Jordan and Rothschild (1915a, b), Wagner (1929) and Ioff et al. (1946).

The relatively weak correlation between the date of flea description and the various biological parameters can also result from confounding factors and events such as, for example, the description of a new species after the revision of a taxon or re-identification of previously misidentified specimens. This could lead to the attribution of a relatively late description date to a host-opportunistic flea species. As a consequence, the resulting relationship between the date of description and the level of host specificity could be wrongly underestimated. The possibility of misidentification of some flea species during field surveys can also not be dismissed. The attribution of a taxon to either the species or subspecies level by different taxonomists with different approaches to the species concept may also influence the results of any search for the biological correlates of the probability of a species being discovered. Finally, flea taxonomy is based mainly on morphological characters. Therefore, in some cases, the existence of cryptic flea species can mask the true patterns of host specificity and, thus, confound the results of studies like ours. However, for the vast majority of flea species, molecular data are not yet available. Despite all these potential sources of background noise, our analyses have revealed that the number of host species used by a flea, as well as how long its principal host has been known to science and how widely distributed it is, influence its probability of being found. By extrapolation, we can infer that the flea species not yet discovered are highly host-specific, and they exploit little-known host species with limited geographic distribution.

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References

Alania II, Rostigaev BA, Shiranovich PI, Dzneladze MT (1964) Data on the flea fauna of Adzharia. Proc Armenian Anti-Plague Station 3:407–435 (in Russian)

Allred DM (1968) Fleas of the national reactor testing station. Great Basin Nat 28:73–87

Allsop PG (1997) Probability of describing an Australian scarab beetle: influence of body size and distribution. J Biogeogr 24:717–724

Blackburn TM, Gaston KJ (1995) What determines the probability of discovering a species? A study of South American oscine passerine birds. J Biogeogr 22:7–14

Burdelova NV (1996) Flea fauna of some small mammals in Dzhungarskyi Alatau. In: Burdelov LA (ed) Proceeding of the conference ''ecological aspects of epidemiology and epizootology of plague and other dangerous diseases.'' Middle Asian Science Anti-Plague Institute, Almaty, Kazakhstan, pp 119–120 (in Russian)

Cabrero-Sanudo FJ, Lobo JM (2003) Estimating the number of species not yet described and their characteristics: the case of the Western Palaearctic dung beetle species (Coleoptera, Scarabaeoidea). Biodivers Conserv 12:147–166

Collen B, Purvis A, Gittelman JL (2004) Biological correlates of description date in carnivores and primates. Global Ecol Biogeogr 13:459–467

Davis RM, Smith RT, Madon MB, Sitko-Cleugh E (2002) Flea, rodent and plague ecology at Chichupate Campground, Ventura County, California. J Vector Ecol 27:107–127

Elshanskaya NI, Popov MN (1972) Zoologico-parasitological characteristics of the river Kenkeme valley (Central Yakutia). In: Kolosova LD, Lukyanova IV (eds) Theriology, vol 1. Nauka Publishing House Siberian Branch, Novosibirsk, USSR, pp 368–372 (in Russian)

Emelyanova ND, Shtilmark FR (1967) Fleas of insectivores, rodents and lagomorphs of the central part of Western Sayan. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 27:241–253 (in Russian)

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Garland T Jr, Harvey PH, Ives AR (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. Am Nat 41:18–32

Garland T Jr, Dickerman AWC, Janis M, Jones JA (1993) Phylogenetic analysis of covariance by computer simulation. Syst Biol 42:265–292

Gaston KJ (1991) Body size and probability of description: the beetle fauna of Britain. Ecol Entomol 16:505–508

Gaston KJ, Blackburn TM (1994) Are newly described bird species small bodied? Biodivers Lett 2:16–20

Gaston KJ, Blackburn TM, Loder N (1995) Which species are described first? The case of North American butterflies. Biodivers Conserv 4:119–127

Harvey PH, Pagel MD (1991) A comparative method in evolutionary biology. Oxford University Press, Oxford

Heywood VH, Watson RT (1995) Global biodiversity assessment. Cambridge University Press, Cambridge

Hopkins GHE, Rothschild M (1953) An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vol I. Tungidae and Pulicidae. Trustees British Museum, London

Hopkins GHE, Rothschild M (1956) An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vol II. Coptopsyllidae, Vermipsyllidae, Stephanocircidae, Ischnopsyllidae, Hypsophthalmidae and Xiphiopsyllidae. Trustees British Museum, London

Hopkins GHE, Rothschild M (1962) An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vol III. Hystrichopsyllidae. Trustees British Museum, London

Hopkins GHE, Rothschild M (1966) An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vol IV. Hystrichopsyllidae. Trustees British Museum, London

Hopkins GHE, Rothschild M (1971) An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vol V. Leptopsyllidae and Ancistropsyllidae. Trustees British Museum, London

Ioff IG, Tiflova VE, Argyropulo AI, Fedina OA, Dudolkina LA, Shiranovich PI (1946) News species of fleas (Aphaniptera). Med Parasitol 15:85–94 (in Russian)

Jordan K, Rothschild NC (1915a) On some Siphonaptera collected by W. Ruckbeil in East Turkestan. Ectoparasites 1:1–24

Jordan K, Rothschild NC (1915b) Contribution to our knowledge of American Siphonaptera. Ectoparasites 1:45–60

Koshkin SM (1966) Data on the flea fauna in the Sovetskaya Gavan. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 26:242–248 (in Russian)

Kozlovskaya OL (1958) Flea (Aphaniptera) fauna of rodents from of the river Ussury valley in the Khabarovsk region. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 17:109–116 (in Russian)

Krasnov BR, Shenbrot GI, Medvedev SG, Vatschenok VS, Khokhlova IS (1997) Host-habitat relations as an important determinant of spatial distribution of flea assemblages (Siphonaptera) on rodents in the Negev Desert. Parasitology 114:159–173

Krasnov BR, Shenbrot GI, Khokhlova IS, Degen AA (2004) Ectoparasite species richness and characteristics of host body, host geography and host "milieu". J Anim Ecol 73:1121–1128

Kunitsky VN, Kunitskaya NT (1962) Fleas of the southwestern Azerbaijan. Proc Azerbajanian Anti-Plague Station 3:156–169 (in Russian)

Labunets NF (1967) Zoogeographic characteristics of the western Khanday. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 27:231240–231341 (in Russian)

Leonov YA (1958) Fleas parasitic on rodents of the southern part of Primorye (Far East). Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 17:147–152 (in Russian)

Letov GS, Emelyanova ND, Letova GI, Sulimov AD (1966) Rodents and their ectoparasites in the settlements of Tuva. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 26:270–276 (in Russian)

Linsdale JM, Davis BS (1956) Taxonomic appraisal and occurrence of fleas at the Hastings Reservation in Central California. Univ Calif Publ Zool 54:293–370

Maddison WP, Maddison DR (2004) Mesquite: a modular system for evolutionary analysis. Version 1.04. http://mesquiteproject.org

Martinez-Meyer E, Peterson AT, Hargrove WW (2004) Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. Global Ecol Biogeogr 13:305–314

Medellin RA, Soberon J (1999) Predictions of mammal diversity on four land masses. Conserv Biol 13:143–149

Medvedev SG (1998) Classification of fleas (order Siphonaptera) and its theoretical foundations. Entomol Rev 78:511–521

Medvedev SG, Lobanov AL (1999) Information-analytic system of the World fauna of fleas (Siphonaptera): results and prospects of development. Entomol Rev 79:654–665

Midford PE, Garland T Jr, Maddison WP (2003) PDAP:PDTREE package for Mesquite, Version 1.00. http://mesquiteproject.org/pdap_mesquite/index.html

Mikulin MA (1958) Data on fleas of the Middle Asia and Kazakhstan. 5. Fleas of the Tarbagatai. Proc Middle Asian Sci Anti-Plague Inst 4:227–240 (in Russian)

Mikulin MA (1959a) Data on fleas of the Middle Asia and Kazakhstan. 10. Fleas of the eastern Balkhash desert, Trans-Alakul desert and Sungorian Gates. Proc Middle Asian Sci Anti-Plague Inst 6:205–220 (in Russian)

Mikulin MA (1959b) Data on fleas of the Middle Asia and Kazakhstan. 8. Fleas of the Akmolinsk region. Proc Middle Asian Sci Anti-Plague Inst 5:237–245 (in Russian)

de Moraes LB, Bossi DEP, Linhares AX (2003) Siphonaptera parasites of wild rodents and marsupials trapped in three mountain ranges of the Atlantic forest in southeastern Brazil. Mem Inst Oswaldo Cruz 98:1071–1076

Morlan HB (1955) Mammal fleas of Santa Fe County, New Mexico. TX Rep Biol Med 13:93–125

Morozkina EA, Lysenko LS, Kafarskaya DG (1971) Fleas of the red marmot (*Marmota caudata*) and other animals inhabiting the Gissar ridge. Probl Particularly Dangerous Infect (Works Anti-Plague Establishments) 1(17):38–44 (in Russian)

Nazarova IV (1981) Fleas of the Volga–Kama region. Nauka Publishing House, Moscow, USSR (in Russian)

Pagel M (1992) A method for the analysis of comparative data. J Theor Biol 156:431–442

Paramonov BB, Emelyanova ND, Zarubina VN, Kontrimavitchus VL (1966) Materials for the study of ectoparasites of rodents and shrews of the Kamchatka peninsula. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 26 333–341 (in Russian)

Pauller OF, Elshanskaya NI, Shvetsova IV (1966) Ecological and faunistical review of mammalian and bird ectoparasites in the tularemia focus of the Selenga river delta. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 26:322–332 (in Russian)

Peterson AT, Soberon J, Sanchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267

Popova AS (1968) Flea fauna of the Moyynkum desert. In: Fenyuk BK (ed) Rodents and their ectoparasites. Saratov University Press, Saratov, USSR, pp 402–406 (in Russian)

Poulin R (1996) How many parasite species are there: are we close to answers? Int J Parasitol 26:1127–1129

Poulin R (2002) The evolution of monogenean diversity. Int J Parasitol 32:245–254

Poulin R, Mouillot D (2003) Parasite specialization from a phylogenetic perspective: a new index of host specificity. Parasitology 126:473–480

Reshetnikova PI (1959) Flea fauna of the Kustanai region. Proc Middle Asian Sci Anti-Plague Inst 6:261–265 (in Russian)

Rothschild NC (1915a) A synopsis of the British Siphonaptera. Entomol Mon Mag 51:49–112

Rothschild NC (1915b) On *Neopsylla* and some allied genera of Siphonaptera. Ectoparasites 1:30–44

Sapegina VF, Lukyanova IV, Fomin BN (1981) Fleas of small mammals in northern foothills of Altai Mountains and Upper Ob river region. In: Maximov AA (ed) Biological problems of natural foci. Nauka Publishing House Siberian Branch, Novosibirsk, USSR, pp 167–176 (in Russian)

Shwartz EA, Berendiaeva EL, Grebenyuk RV (1958) Fleas of rodents of the Frunze region. Proc Middle Asian Sci Anti-Plague Inst 4:255–261 (in Russian)

Sineltschikov VA (1956) Study of flea fauna of the Pavlodar region. Proc Middle Asian Sci Anti-Plague Inst 2:147–153 (in Russian)

Smit FGAM (1987) An illustrated catalogue of the Rothschild collection of fleas (Siphonaptera) in the British Museum (Natural History), vol V. Malacopsylloidea (Malacopsyllidae and Rhopalopsyllidae). Oxford University Press, British Museum (Nat Hist), Oxford, London

Smith FA, Brown JH, Haskell JP, Lyons SK, Alroy J, Charnov EL, Dayan T, Enquist BJ, Ernest SKM, Hadly EA, Jones KE, Kaufman DM, Marquet PA, Maurer BA, Niklas KJ, Porter WP, Tiffney B, Willig MR (2004) Similarity of mammalian body size across the taxonomic hierarchy and across space and time. Am Nat 163:672–691

Stanko M, Miklisova D, Gouy de Bellocq J, Morand S (2002) Mammal density and patterns of ectoparasite species richness and abundance. Oecologia 131:289–295

Syrvacheva NG (1964) Data on the flea fauna of Kabardino–Balkarian ASSR. Proc Armen Anti-Plague Station 3:389–405 (in Russian)

Traub R, Rothschild M, Haddow JF (1983) The Ceratophyllidae: key to the genera and host relationships. Cambridge University Press, Cambridge

Vasiliev GI (1966) On ectoparasites and their hosts in relation to the plague epizootic in Bajan–Khongor aimak (Mongolian People Republic). Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 26:277–281 (in Russian)

Vershinina TA, Lyamkin VF, Kryukov IL (1967) Fleas of small mammals in the Barguzin depression and their landscape distribution. Proc Irkutsk State Sci Anti-Plague Inst Siberia Far East 27:265–278 (in Russian)

Violovich NA (1969) Landscape and geographic distribution of fleas. In: Maximov AA (ed) Biological regionalization of the Novosibirsk region. Nauka Publishing House Siberian Branch, Novosibirsk, USSR, pp 211–221 (in Russian)

Wagner J (1929) About new species of Palaearctic fleas (Aphaniptera) II. Ann Rep Zool Mus USSR Acad Sci 30:531–547 (in Russian)

Webb TJ, Gaston KJ (2003) On the heritability of geographic range sizes. Am Nat 161:553–566

Wilson EO (2003) The encyclopedia of life. Trends Ecol Evol 18:77–80

Wilson DE, Reeder DM (eds) (1993) Mammal species of the world: a taxonomic and geographic reference. Smithsonian Inst Press, Washington

Yudin BS, Krivosheev VG, Belyaev VG (1976) Small mammals of the northern Far East. Nauka Publishing House Siberian Branch, Novosibirsk, USSR (in Russian)

Zagniborodova EN (1960) Fauna and ecology of fleas on the western Turmenistan. In: Fenyuk BK (ed) Problems of natural foci and epizootology of plague in Turkmenistan. Turkmenian Anti-Plague Station, All-Union Sci Anti-Plague Inst “Microb”, Saratov, USSR, pp 320–334 (in Russian)