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Character combinations, convergence and diversification in ectoparasitic arthropods

Robert Poulin *

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

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ABSTRACT

Different lineages of organisms diversify over time at different rates, in part as a consequence of the characteristics of the species in these lineages. Certain suites of traits possessed by species within a clade may determine rates of diversification, with some particular combinations of characters acting synergistically to either limit or promote diversification; the most successful combinations may also emerge repeatedly in different clades via convergent evolution. Here, the association between species characters and diversification is investigated amongst 21 independent lineages of arthropods ectoparasitic on vertebrate hosts. Using nine characters (each with two to four states) that capture general life history strategy, transmission mode and host-parasite interaction, each lineage was described by the set of character states it possesses. The results show, firstly, that most possible pair-wise combinations of character states have been adopted at least once, sometimes several times independently by different lineages; thus, ectoparasitic arthropods have explored most of the life history character space available to them. Secondly, lineages possessing commonly observed combinations of character states are not necessarily the ones that have experienced the highest rates of diversification (measured as a clade's species-per-genus ratio). Thirdly, some specific traits are associated with higher rates of diversification. Using more than one host per generation, laying eggs away from the host and intermediate levels of fecundity are features that appear to have promoted diversification. These findings indicate that particular species characters may be evolutionary drivers of diversity, whose effects could also apply in other taxa.

1. Introduction

The distribution of living species amongst higher taxa shows clearly that rates of diversification vary greatly from clade to clade. This is certainly the case for parasitic organisms, with some taxonomic groups of parasites being orders of magnitude more speciose than others (Poulin and Morand, 2004). Simulation studies have confirmed that the unequal diversity of different clades cannot be accounted by null models in which speciation rates are roughly equal amongst higher taxa (Dial and Marzluff, 1989; Slowinski and Guyer, 1989; Nee et al., 1996; Owens et al., 1999). Instead, the differential evolutionary success of different clades may be driven by environmental factors (Davies et al., 2004). Alternatively, diversification often appears linked to intrinsic properties of the species within clades, with some clades possessing traits that enhance rates of speciation, limit the risk of extinction, or both (Marzluff and Dial, 1991; Slowinski and Guyer, 1993; Barraclough et al., 1998; Phillimore et al., 2006; Ricklefs, 2007). For instance, small body size and the traits that correlate with it can promote higher net rates of diversification (Kozlowski and Gawelczyk, 2002).

Although individual traits can influence the probabilities of speciation or extinction, it is the whole suite of traits possessed by species within a clade that will determine rates of diversification. The influences of different traits may cancel each other out, or act synergistically to exert a greater impact on diversification. Trait combinations that favour diversification may thus be similar to adaptive peaks (*sensu* Wright, 1984): suites of traits that 'work best together', i.e. that confer on a clade the highest likelihood of persisting and diversifying, may represent the most likely end-points of convergent evolution. Through some form of higher-level selection (Williams, 1992), clades possessing these suites of traits may come to outnumber those possessing other trait combinations associated with lower diversification success. One could test this hypothesis by looking for a correlation, across related clades, between the within-clade diversification rates and the relative commonness of the trait combinations shown by each clade. Along those lines, Ricklefs (2005) has found that passerine clades consisting of relatively few species exhibit morphological measurements that depart from the most common values reported for passerines in general, which places them on the margins of the group's morphological parameter space.

Here, the diversification rates of several independent clades, or lineages, of arthropods ectoparasitic on vertebrate hosts are related to their suite of life history traits and other characters associated with transmission mode and interaction with the host. Although transitions to parasitism have occurred frequently and independently amongst arthropods, all parasitic lineages still share the

* Tel.: +64 3 479 7983; fax: +64 3 479 7584.
E-mail address: robert.poulin@stonebow.otago.ac.nz

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same basic constraints characterising their phylum (e.g., exoskeleton and moulting, segmentation, jointed limbs), and all lineages considered in this study exploit hosts belonging to the same class (Vertebrata). Nevertheless, they exhibit a broad range of lifestyles, and counts of known diversity for these groups span two orders of magnitude. Most statistical methods used to link biological features and rates of diversification require a well-resolved phylogeny, in order to assess the branching rates in different parts of the tree (Barraclough et al., 1998; Maddison et al., 2007; Ricklefs, 2007). There is no comprehensive within-clade phylogeny for the vast majority of arthropod lineages considered here. However, their separate and independent origins mean that they can be treated as independent statistical observations, and comparisons can be made amongst clades using overall rates of diversification.

The specific objectives of this study are (i) to characterise the various lineages by the suite of traits they possess, and determine whether lineages possessing the most widely used combinations of character states are also the ones that have experienced the highest rates of diversification; and (ii) to determine which, if any, specific character is associated with high rates of diversification. This is the first attempt to link suites of traits to broad patterns of diversification across many parasitic lineages, and it sheds new light on some evolutionary drivers of parasite diversity.

2. Materials and methods

Diversity and life history data were compiled for 21 lineages of arthropods ectoparasitic on vertebrates (Table 1). These all consist of 'true' parasites involved in long-term or permanent associations with vertebrate hosts, and displaying considerable morphological and physiological adaptations to their parasitic lifestyle. The analysis therefore excludes groups that make only brief feeding visits on vertebrates, such as many blood-sucking dipterans (e.g. mosquitoes); these are often labelled as micropredators rather than parasites (Lafferty and Kuris, 2002). In addition, the analyses did not consider groups that are sometimes referred to as ectoparasitic but are in fact endoparasitic (e.g. bot flies), and thus not exposed to host grooming and other external conditions. Also excluded are a few groups consisting of very few species (<5 generally), representing unusual cases of parasitism within an otherwise non-parasitic clade, and thus not successful adoptions of parasitism by an entire lineage. The 21 lineages included here are treated as representing independent transitions to a mode of life involving obligate feeding on vertebrates, based on existing phylogenetic evidence (see below). The monophyletic status of some of these groups is not clearly established (in particular mites and lice; see references in Table 1). In addition, the presumed phylogenetic independence of some groups rests on cladistic hypotheses that require further validation (e.g. families within the copepod clade Poecilostomatoidea; see Ho, 1991; Poulin, 1995; Boxshall and Halsey, 2004). Nevertheless, the 21 lineages included here are treated as statistically independent groups (but see below) because they comprise species sharing similar life history characteristics that are generally considered as issued from single phylogenetic transitions to parasitism on vertebrates.

The number of known species and the number of genera were obtained for each lineage from recent taxonomic revisions and compilations (see references in Table 1). When two estimates were available for one group, the highest values were used. The number of distinct species in a lineage must increase over time in a growing clade, as the clade diversifies (Ricklefs, 2007). The age of each clade may thus be a key predictor of variation in species richness amongst clades; however, estimates of clade age are unavailable for most lineages included in this study. Therefore, the ratio of number of species to number of genera was used as a measure of diversification within-clade; the number of species-per-genus is likely to provide an index of speciation rates close to the branch tips in the phylogenetic tree independent of how long ago a lineage has made the transition to parasitism. Because genera are subjective taxonomic constructs, species-to-genus ratios are not ideal measures of diversification; in the absence of species-level phylogenies, however, they provide the best index available.

Table 1
List of taxa used in the analysis, their species and generic diversity, and the main sources of information on their biology and diversity.

Taxon	Common name	No. species	No. genera	Sources[a]
Crustacea				
Branchiura	Fish lice	175	4	1, 2
Cyamidae	Whale lice	23	6	3, 4
Gnathiidae	Isopods	171	10	2, 4, 5, 6, 7
Cymothoidae	Isopods	337	41	2, 4, 5
Bomolochidae/Telsidae	Copepods	105	18	8, 9
Philichthyidae	Copepods	54	9	8, 9
Ergasilidae	Copepods	262	25	8, 9
Chondracanthidae/Lernaeosoleidae	Copepods	162	46	8, 9
Siphonostomatoidea less Pennellidae	Copepods	1144	141	8, 9
Pennellidae	Copepods	103	20	8, 9
Lernaeidae	Copepods	116	16	8, 9
Arachnida				
Ixodida	Ticks	889	17	4, 10, 11
Dermanyssoidea	Mesostigmatan mites	1359	273	12, 13, 14
Psoroptida	Scab/mange mites, feather/fur mites	2022	667	12, 13, 15
Trombiculoidea	Chiggers	1109	171	12, 13, 16
Insecta				
Siphonaptera	Fleas	2891	241	4, 17
Amblycera	Chewing lice	1341	95	18
Ischnocera	Chewing lice	3120	157	18
Anoplura	Sucking lice	532	49	19, 20
Streblidae	Bat flies	227	32	21
Nycteribiidae	Bat flies	275	12	21

[a] 1, Boxshall (2005); 2, Kearn (2004); 3, Lützen (2005); 4, Catalogue of Life (http://www.catalogueoflife.org/info_2008_checklist.php); 5, Lester (2005); 6, Tanaka and Aoki (2000); 7, Smit et al. (2003); 8, Boxshall and Halsey (2004); 9, Poulin (1995); 10, Oliver (1989); 11, Durden (2006); 12, Synopsis of the Described Arachnida of the World (http://insects.tamu.edu/research/collection/hallan/Acari/0ReportHi.htm); 13, Walter and Proctor (1999); 14, Dowling (2006); 15, Arlian (1989); 16, Shatrov and Kudryashova (2006); 17, Medvedev and Krasnov (2006); 18, Price et al. (2003); 19, Durden and Musser (1994); 20, Kim (2006); 21, Dick and Patterson (2006).

Table 2
List of the characters (and their possible states) used to categorise the various arthropod taxa used in the analysis.

Characters	Code	State
Parasitic life	1	All feeding done parasitically
	2	Feeding non-parasitically at some stage
Attachment	1	Anchored fixedly
	2	Can move on the surface of the host
Association with the host	1	Use more than one host individual throughout their life (multiple infections/lifetime)
	2	Use a single host individual throughout their life
Egg laying	1	Eggs released and/or deposited on substrate away from host
	2	Eggs laid and hatching on the host
Infective stages	1	Mobile infective stages capable of host location
	2	Infective stages not mobile, all transmission via host–host contact
Lifetime fecundity	1	$<10^2$ eggs
	2	10^2 to 10^3 eggs
	3	10^3 to 10^4 eggs
Modal body size	1	About 1 mm
	2	About 5 mm
	3	About 10 mm
	4	From 50 to 100 mm
Type of host	1	Ectotherm
	2	Endotherm
Habitat	1	Aquatic
	2	Terrestrial

For each lineage, information was also obtained on nine characters that capture the general life history strategy, transmission mode and host-parasite interaction of species within the lineage. Each character has two to four states (Table 2) defined so as to be unambiguous, and intended to include all possibilities observed in nature. Discrete characters that vary within-clades (such as the nature of the host tissue (skin, blood, etc.) on which the parasites feed, which varies amongst related copepod species and in other groups, too) were not considered, and therefore all nine characters appear to be true clade traits. Thus, each of the 21 lineages can be described by a formula consisting of the set of character states it possesses (Table 3). It is for this reason that the copepod family Pennellidae is treated as a separate lineage from other siphonostomatoid families (Tables 1 and 3). Pennellids possess a distinct set of character states: they are unique amongst siphonostomatoids in using a two-host life cycle, in which juvenile copepods detach from their original pelagic mollusc or fish host to transfer to a different fish species on which they mature (Boxshall and Halsey, 2004). Thus, although pennellids do not represent an independent transition to parasitism, they are treated as one because they show a clear departure from the typical siphonostomatoid life history strategy.

Following the approach of Thomas and Reif (1993), the complete set of combinations of the character states listed in Table 2 across all lineages is taken to represent the life history character space of ectoparasitic arthropods. By considering characters two at a time, one obtains a two-dimensional matrix of 194 pair-wise combinations of the character states that are theoretically possible (Fig. 1). The frequency at which any of these 194 combinations are observed amongst the 21 lineages provides a measure of how often a particular combination of features has been adopted by lineages sharing the same ectoparasitic mode of life. Some lineages possess many 'popular' pair-wise combinations of character states (i.e. combinations seen in many of the 21 lineages; see Fig. 1), whereas others possess few. By summing the frequency values in each of the cells of the life history character matrix that correspond to combinations seen in a particular lineage, a 'convergence score' can be generated for that lineage: a high value indicates that a lineage has adopted character combinations also observed in many other lineages, whereas a low value indicates that a lineage displays character combinations that are relatively uncommon.

To verify that diversification rates in each of the 21 lineages were independent of each other, for example that lineages of crustaceans did not all diversify at similarly high rates compared to insect lineages, a test for the independence of character evolution was implemented using the PDAP:PDTREE module (Midford, P.E., Garland, T. Jr., Maddison, W.P., 2007. PDAP:PDTREE package for Mesquite, Version 1.1. http://mesquiteproject.org/pdap_mesquite/

Table 3
Character states for the arthropod taxa used in the analysis, for each of the nine characters (see Table 2 for definitions of character states).

Taxon	Parasitic life	Attachment	Association with the host	Egg laying	Infective stages	Lifetime fecundity	Modal body size	Type of host	Habitat
Crustacea									
Branchiura	1	2	1	1	1	2	2	1	1
Cyamidae	1	2	2	2	2	3	3	2	1
Gnathiidae	1	2	1	1	1	1	2	1	1
Cymothoidae	1	2	2	2	1	3	4	1	1
Bomolochidae/Telsidae	1	1	2	2	1	3	1	1	1
Philichthyidae	1	1	2	2	1	3	1	1	1
Ergasilidae	1	1	2	2	1	2	1	1	1
Chondracanthidae/Lernaeosoleidae	1	1	2	2	1	3	2	1	1
Siphonostomatoidea less Pennellidae	1	1[a]	2	2	1	3	3	1	1
Pennellidae	1	1	1	2	1	3	3	1	1
Lernaeidae	1	1	2	2	1	3	3	1	1
Arachnida									
Ixodida	1	1	1	1	1	2	2	2	2
Dermanyssoidea	2	2	1	1	1	1	1	2	2
Psoroptida	1	1	2	2	2	1	1	2	2
Trombiculoidea	2	1	2	1	1	2	1	2	2
Insecta									
Siphonaptera	1	2	1	1	1	2	2	2	2
Amblycera	1	2	2	2	2	1	1	2	2
Ischnocera	1	2	2	2	2	1	1	2	2
Anoplura	1	2	2	2	2	1	1	2	2
Streblidae	1	2	1	1	1	1	1	2	2
Nycteribiidae	1	2	1	1	1	1	1	2	2

[a] Movement on the host surface is possible in some siphonostomatoid families, e.g. Caligidae.

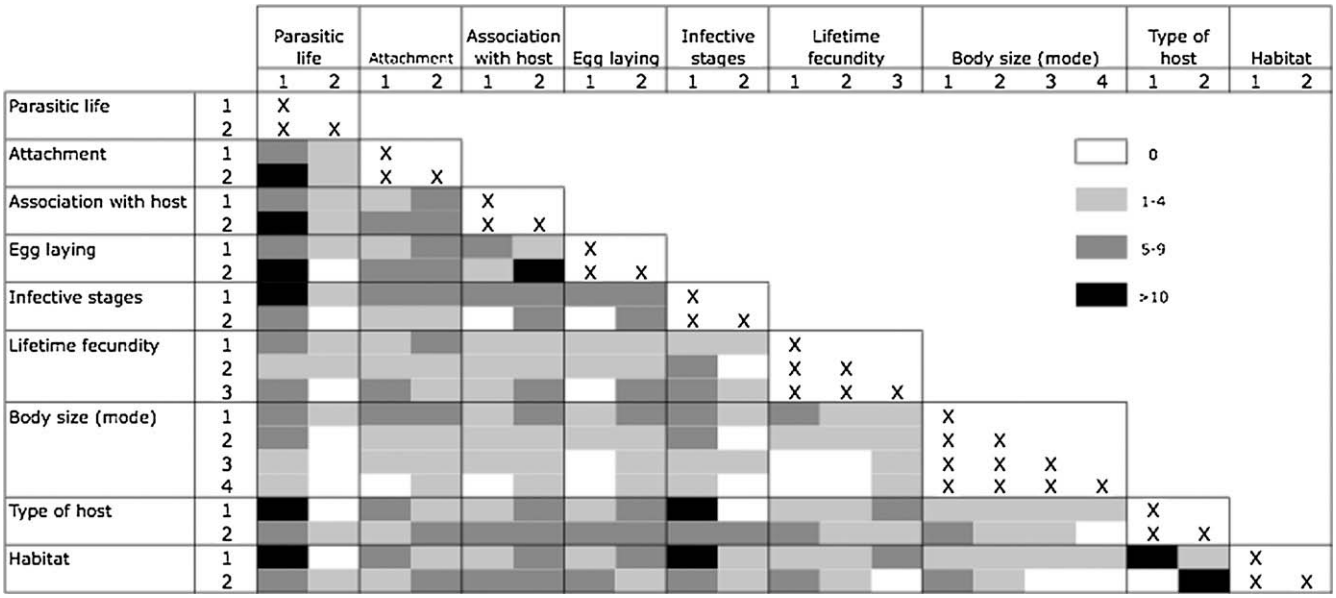

Fig. 1. Matrix of all 194 possible pair-wise combinations of character states representing the life history character space for ectoparasitic arthropods. The frequency of occurrence of each combination is indicated by the shading of the cell: the darker the colour, the more frequently that combination is observed.

index.html) implemented in Mesquite Modular System for Evolutionary Analysis (Maddison, W.P., Maddison, D.R., 2007. Mesquite: A Modular System for Evolutionary Analysis, Version 2.01. http://mesquiteproject.org). The test consisted in comparing the distribution of log-transformed species-per-genus ratio values amongst the 21 branch tips corresponding to the different lineages in a phylogenetic tree, to a random distribution. Independent contrasts (Felsenstein, 1985) were computed, and their average (absolute) value was compared to that of contrasts generated following random permutations of ratio values amongst branch tips: an observed average value significantly lower than those obtained from random permutations would indicate clustering of similar ratio values in certain parts of the tree. The phylogenetic relationships amongst the 21 lineages were inferred from Hassanin (2006) and additional sources from the Tree of Life (http://tolweb.org/tree/).

The relationship between convergence scores, obtained from the life history character matrix, and species-per-genus ratios was tested across the 21 lineages using a Pearson product-moment correlation; for this and subsequent analyses, species-per-genus ratios were log-transformed to meet the assumptions of parametric tests. To make sure that this relationship was not dependent on phylogenetic relationships amongst the lineages, the correlation analysis was repeated using the phylogenetically independent contrast method (Felsenstein, 1985). As above, a tree representing the relationships amongst the 21 lineages was derived from the molecular phylogeny of Hassanin (2006). Independent contrasts were computed on log-transformed data using the PDAP:PDTREE module implemented in Mesquite. The relationship was forced through the origin, and all other procedures follow Garland et al. (1992).

In addition, to pinpoint which of the nine characters are most closely associated with species diversification, species-per-genus ratios (dependent variable) were compared amongst lineages that displayed different character states, using separate one-way ANOVAs for each of the characters. Following these exploratory univariate analyses, all characters for which significant ($P < 0.05$) effects were detected were then included in multifactorial ANOVAs; the best model, i.e. the one including the subset of characters that explained the most variance in species-per-genus ratios, was retained as providing the best evolutionary explanation of diversity.

3. Results

The number of known species ranged from 23 to 3120 amongst the lineages considered in this analysis. More importantly, species-per-genus ratios ranged from about three to over 50, suggesting that rates of speciation may vary greatly amongst the 21 arthropod lineages. In addition, the distribution of species-per-genus ratio values amongst the tips in the phylogeny of the 21 lineages did not differ from a random distribution ($P = 0.24$ based on 100 permutations), so that rates of diversification in these groups of ectoparasites are independent of phylogenetic influences.

Most of the 194 cells in the matrix of all possible pair-wise combinations of character states are filled, indicating that most pair-wise combinations of character states are realised amongst ectoparasitic arthropods (Fig. 1). Some empty cells represent impossible combinations. For instance, in taxa that lay their eggs away from the host, the only possible type of infective stages are mobile ones capable of host location: egg laying state 1 and infective stages state 2 are therefore not a biologically possible combination (Table 2 and Fig. 1). In other cases, cells with few or no recorded examples indicate character states that have not evolved often amongst parasitic arthropods: for instance, there are generally few taxa without mobile infective stages, or with relatively large body sizes (Fig. 1).

The convergence scores measuring the tendency of a lineage to share particular combinations of character states with few or many other lineages ranged from 162 to 293. This observed range falls toward the highest part of the full possible range of 63–312 for this index, derived from the matrix of realised combinations (Fig. 1). However, the observed scores did not correlate significantly with the species-per-genus ratios measuring rates of diversification within lineages ($r = 0.269$, $P = 0.237$). The same was true when the analysis was repeated using phylogenetically independent contrasts ($r = 0.135$, $P = 0.569$).

For three characters, lineages with one character state had significantly higher species-per-genus ratios than lineages with another character state (Fig. 2). First, lineages in which parasites use more than one host individual throughout their life have higher species-per-genus ratios than those where a single host individual is used ($F_{1,19} = 4.86$, $P = 0.040$). Second, lineages in which eggs

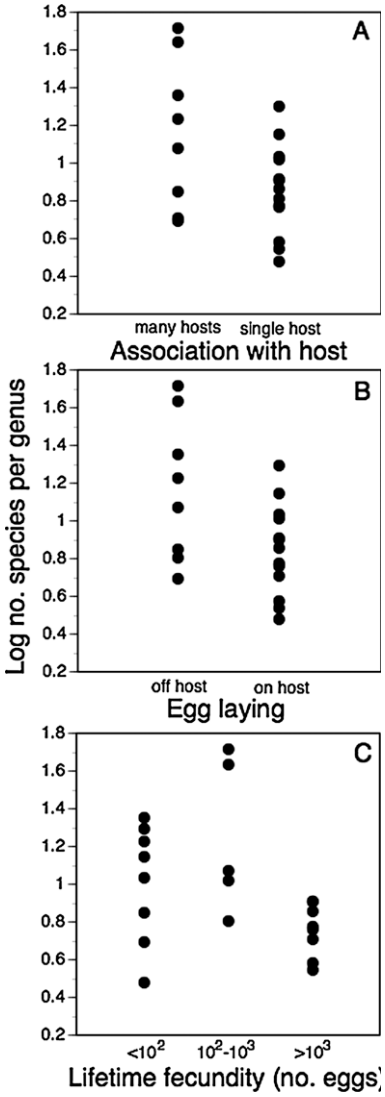

Fig. 2. Ratios of number of species to number of genera for each of 21 lineages of ectoparasitic arthropods, grouped according to whether they use one or more hosts throughout their life (A), whether they lay their eggs off or on their host (B), and based on their typical lifetime fecundity (C).

are deposited on substrate away from the host have higher species-per-genus ratios than those in which eggs are laid and hatch on the host ($F_{1,19} = 5.74$, $P = 0.027$). Third, lineages in which species have intermediate fecundity show higher species-per-genus ratios than those with either lower or greater fecundity ($F_{2,18} = 4.78$, $P = 0.022$). When combining these characters as predictor variables, the best model included only host association, i.e. using a single host or more than one, and lifetime fecundity (whole model: $F_{3,17} = 3.83$, $P = 0.029$), and explained 40% of the variance in species-per-genus ratios amongst the 21 lineages.

4. Discussion

Using a broad definition of parasitism, almost half of the known animal species can be classified as parasites (Windsor, 1998; Poulin and Morand, 2000, 2004). Clearly, lineages adopting a parasitic mode of life have been successful in evolutionary terms. The results of this study explain why certain lineages have been more successful than others by linking rates of diversification with species characters. The present analyses have produced three main findings. First, the various lineages of ectoparasitic arthropods have explored most of the life history character space available to them. As shown by Fig. 1, most possible combinations of traits have been 'discovered' at least once, and sometimes adopted repeatedly by different lineages. Second, lineages possessing many 'popular' combinations of character states are not necessarily the ones that have experienced the highest rates of diversification. Third, particular traits are associated with higher rates of diversification. Specifically, using more than one host per generation and, to a lesser extent, laying eggs away from the host are features that appear to have promoted diversification; in contrast, whilst lifetime fecundity is also important, the most fecund lineages are not those showing the greatest diversification.

Except for combinations that are biologically impossible, it appears that parasitic arthropods have explored most evolutionary possibilities available in the total character space. Yet some combinations of traits have been adopted repeatedly whereas others are only seen in one or very few lineages. The highly 'popular' combinations may be the result of physical/biological constraints and/or convergent evolution. For example, physical contacts amongst fish are less frequent and of shorter duration than amongst mammals or birds, constraining ectoparasites of fish to use mobile infective stages for transmission. Along the same lines, although large-bodied ectoparasites are a priori equally viable on ectothermic or endothermic vertebrates, the greater grooming abilities of birds and mammals (compared to fish or amphibians) may have selected for smaller ectoparasite body sizes on these hosts. Whatever the reasons for the high frequency at which certain combinations of traits have been adopted, some of them may represent fixed point attractors within the character space (see Thomas and Reif, 1993), i.e. points toward which arthropod ectoparasite life history strategies evolve because of their adaptive value.

Nevertheless, lineages having many of these widespread combinations of character states were not the ones showing the highest rates of diversification. This finding contrasts with that of Ricklefs (2005), who found that the most speciose clades of passerine birds were those with morphological measurements closest to the group's overall average values. Instead, in the present study, the highest rates of diversification in parasitic arthropods were associated with the possession of a few specific traits, regardless of all other traits. Lineages in which the parasites require more than one host individual to complete their life cycle have experienced higher rates of diversification. Although the different host individuals are usually of the same species, multiple infection events per generation increase the chances of contacting other host species that may be suitable for the parasite. Opportunities for transmission to other host species on a microevolutionary timescale are the major determinants of host switching in parasites over macroevolutionary time (e.g., Clayton and Johnson, 2003; Poulin, 2007). Parasites that colonise new host species are more likely to subsequently speciate, and lineages in which this is frequent will experience higher rates of diversification. Thus association with multiple host individuals from hatching to death, including periodic detachment from the host for egg laying followed by re-infection, are traits clearly linked with coevolutionary and diversification processes. Lifetime fecundity also emerged as an important character associated with higher rates of diversification, a finding that differs from analyses on some other taxa (e.g. Owens et al., 1999; Stuart-Fox and Owens, 2003). The reason why arthropod lineages showing the highest average fecundity (>10^3 eggs) were not the ones with the highest rates of diversification may be that these lineages generally use a single host per life cycle and lay their eggs on the host (see Fig. 1), both traits associated with lower diversification.

The potential diversification of a lineage is not solely dependent on the intrinsic properties of its species, but also on external factors controlling the opportunities for speciation. For instance, in biogeographical surveys, the regional species richness of ectoparasitic fleas is strongly correlated with the regional richness of potential mammalian host species (Krasnov et al., 2004, 2007). The number of species in local parasite assemblages is the outcome of ecological processes, but the number of available host species may also limit opportunities for diversification in particular lineages over evolutionary time. Thus the diversity of the particular host taxa exploited by a parasite lineage may constrain its eventual diversification. Since the parasite lineages examined here may only be capable of using a subset of hosts within the larger group that they exploit (e.g. only some orders or families of fish or birds), it is difficult to determine exactly their actual range of possible hosts. This variable cannot therefore easily be incorporated into the analyses. Nevertheless, although the size of the host pool may explain a significant proportion of the variance in rates of diversification, it does not negate the effect of parasite traits uncovered in this study.

The analyses presented here are very sensitive to the way in which the rates of diversification have been measured. It would be pointless to use current numbers of described species, on their own, since these are likely to greatly underestimate true species richness (Poulin and Morand, 2000, 2004). Frequency of branching and tree structure are also not an option since phylogenies are unavailable for most of the groups studied here. The ratio of number of known species to number of genera provides an estimate of the relative number of speciation events per higher branch in the phylogeny of each of the 21 lineages, at least for the most recent part of their evolutionary history. Of course, this assumes that the concept of a "genus" is equally applied across taxa, which may not be the case as the taxonomy of some groups dates back to pre-cladistic days. There may be differences amongst taxonomic specialists for these different groups regarding tendencies to lump or split taxa that could influence the species-to-genus ratio; however, these are extremely unlikely to covary with the life history characters included in the present study in a way that would create artefacts in the analyses.

The few earlier investigations of the possible determinants of parasite diversification have focused almost exclusively on monogeneans (but see Morand, 1996 for a preliminary study on nematodes). Monogeneans are ectoparasitic flatworms found mostly on fish. Brooks and McLennan (1993) suggested that monogeneans have experienced an adaptive radiation that they attributed to a key innovation: the simplification of their life cycle back to a one host cycle. However, this interpretation depends entirely on which phylogenetic hypothesis regarding relationships amongst flatworms one chooses to use, and it does not survive when better-supported phylogenies are used (Rohde, 1996). Other studies of monogenean diversification have ruled out small body size (Poulin, 2002) and strict host specificity (Desdevises et al., 2001) as important factors. One major problem with these studies has been the lack of high-level replication, i.e. the lack of independent lineages that one can use to relate rates of diversification to various features. The present study took advantage of the numerous independent transitions to parasitism on vertebrates that have occurred amongst arthropods to identify a few key drivers of diversification, whose more general importance could now be tested on other groups, such as phytophagous insects.

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