Abstract. Optimal-foraging theory, specifically the "Time-Limited Disperser Model," predicts that animals that can search for resources for a long period will be specialists, whereas animals that have limited search times will be generalists. So far, this model has only been tested within individual species, i.e., among animals of similar physiology and life history. I tested the model across multiple species, using a taxonomically diverse community of arthropods found on exposed tree trunks in northern Germany. I sampled 14 arthropod species from different microhabitat types (various cryptogam species and crevice types) and quantified the microhabitat-niche breadths of species by Simpson index. Then, I used multiple regression analysis across phylogenetically independent contrasts to examine the relationship between microhabitat-niche breadth and traits that can control search time (degree of residence on the trunks, tolerance of abiotic stress, speed of movement, generation time). I found that microhabitat specialists had longer generation times, spent more of their life on the trunks and could move faster than generalists. This allowed specialists to search the trunk for a longer period of time than generalists and to require less time to traverse a given search distance. These three findings supported the Time-Limited Disperser Model. However, specialists were no more tolerant of abiotic stress (i.e., desiccation) than were generalists. That is, specialists could not search the trunk during more adverse climatic conditions than could generalists, contradicting the Time-Limited Disperser Model. Overall, the results supported three out of four predictions of the Time-Limited Disperser Model at an interspecific level. Specialists can search for a long time; generalists are pressed for time.

Key words: Arachnida; behavioral ecology; canopy; constraint; Insecta; life history; microhabitat use; niche breadth; optimal foraging; search time; specialization; Time-Limited Disperser Model.

INTRODUCTION

The ecological specialization of organisms is a key issue in biology because it affects a wide array of biological phenomena from the cellular to the community level (MacNally 1995, Bernays 2001). Organisms differ fundamentally in their degree of ecological specialization (MacNally 1995), and ecologists have suggested very different mechanisms to explain such differences at both the intraspecific and interspecific levels.

Intraspecific differences in the degree of specialization have often been explained by optimal-foraging theory, which assumes that some animals decide to be specialists in order to maximize their benefits and minimize their costs (Jaenike 1990, Krebs and Davies 1996). The decision depends not only on the animal’s environment (Rosenzweig 1987, Farnsworth and Illius 1998, Gratton and Welter 1999), but also on the animal’s time budget. An animal that is limited in its search time should be less specialized than a non-time-limited animal. This prediction is known as the "Time-Limited Disperser Model" (Ward 1986, Jaenike 1990, Maybew 1997 [including his "dynamic programming models"]). The model assumes that the costs of rejecting a suboptimal resource patch are high for a time-limited animal, because that animal may not encounter anything else suitable during its short search period. In order to reduce these "costs of lost opportunities," the time-limited animal thus accepts suboptimal resource types more readily than does a non-time-limited animal (e.g., Levins and MacArthur 1969, Jaenike 1978, Mangel 1987; review in Maybew 1997). Moreover, the time-limited animal should be more reluctant to leave a suboptimal resource patch than is the non-time-limited animal (Krebs and Davies 1996). Similar to other optimal-foraging models, the Time-Limited Disperser Model applies in particular when an animal has to make many decisions, for instance when selecting diet, oviposition sites, or microhabitats (Ward 1986, Krebs and Davies 1996). The Time-Limited Disperser Model has been validated repeatedly (e.g., Prokopy et al. 1994, Backwell and Passmore 1996)—at an intraspecific level, time-limited animals are indeed less specialized than non-time-limited animals.

Interspecific differences in the degree of specialization have usually been explained by physiological or life-history constraints that prevent specialists from be-
ing generalists. First, specialists may be unable to find additional resource types because they are too rare or too difficult to reach (Howe and Westley 1988, Tompkins and Clayton 1999). Second, specialists may simply be unable to perceive additional resource types (Bernays 2001). This constraint may even have a selective advantage because an animal that perceives only minimal information can efficiently process this information neurologically and can quickly come to a decision (Bernays 2001). Third, some specialists may have several physiological or morphological constraints that reduce the efficiency by which they can use certain resource types. For instance, the metabolism of some specialists may be adapted to certain toxic resource types and, therefore, be incapable of efficiently handling most other types (Howe and Westley 1988, Jaenike 1990, Price 1997). Such a constraint may also have a selective advantage because the specialists may live in a competitor-free environment and may coevolve with their host (Ehrlich and Murphy 1988, Jaenike 1990). Specialists may also be incapable of competing effectively for certain resource types or resisting predators concentrated near particular resources, of moving across the surface of certain resource types, or of withstanding the microclimate at their surface (Southwood 1972, Bernays and Garaham 1988). Such morphological and physiological constraints on the efficiency or capability of resource utilization may turn into phylogenetic constraints because species, to a large extent, inherit their morphology and physiology from their ancestors (Harvey and Pagel 1991). Interspecific differences in the degree of specialization have only seldom been explained by constraints that prevent generalists from being specialists. First, generalists may be unable to discriminate between similar resource types, and thus be incapable of specializing on one or another of them (Jaenike 1990). Second, generalists may live in an environment where all resource types are rare or ephemeral, and thus be unable to use them in a specialized manner (Futuyama 1976, 1983, Courtney and Chew 1987).

Despite its success in accounting for intraspecific differences in the degree of specialization, the Time-Limited Disperser Model has not yet been used to explain differences at the interspecific level, e.g., to explain why, within a given environment, some species are more specialized than others. (For applications of other optimal-foraging models to the interspecific level, see Abramsky and Rosenzweig [1991], Kotler and Brown [1999] and various other publications by the same authors.) One may, in fact, argue that the Time-limited Disperser Model is not relevant at the interspecific level. The large differences in physiology and life history of species may override the effect of search-time limitations and decision-optimization of the individual animals. Yet, these very differences in physiology and life history cause differences in the animals’ search-time budgets, and may thereby fundamentally affect their decision making (Jaenike 1990).

The short-term (i.e., daily) search-time budget of a given species depends, in particular, on the following traits: the degree of residency of the animal in a particular environment, the animal’s tolerance of harsh abiotic conditions, and the animal’s speed of movement. First, the duration of residency in an environment controls the time that an animal can search there. Second, the degree of tolerance for harsh abiotic conditions determines whether an animal can search during harsh climatic conditions. Third, the speed of movement controls the time an animal needs to traverse a given search distance; slow-moving animals may run out of search time before they reach their destination. The long-term (i.e., lifetime) search-time budget, in contrast, depends more strongly on a fourth trait, the generation time (excluding sessile stages). Generation time influences, for instance, the time an animal can search for an optimal oviposition site, and Jaenike (1978) and Mangel (1987) have shown that oviposition-site selection of individuals can indeed be determined by search-time limitations. Generation time also influences the life-history strategy of animals. Animals with a short generation time often display only a single, short dispersal phase followed by a rapid reproduction and death, the “r-strategy” (Southwood 1988). The search-time budget of these animals is very limited. Many animals with a long generation time, in contrast, display extensive, repeated migrations, which increase the chance of eventually finding the single optimal resource type for foraging, shelter, or oviposition. Overall, the Time-Limited Disperser Model would predict that specialization of species increases with their residency, their abiotic tolerance, their speed of movement, and their generation time, as all these traits increase the search time available to the animals. Surprisingly, this interspecific prediction has not yet been tested, despite the renewed interest in comparative biology during the last decade (Harvey and Pagel 1991).

In the present study, I tested the prediction of the Time-Limited Disperser Model at an interspecific level. I studied the arthropod species that coexist on the bark of exposed tree trunks in a small region of northern Germany. This community is taxonomically very diverse: it includes Insecta (Collembola, Heteroptera, Psocoptera, Diptera), Arachnida (Araneae, oribatid mites, trombidiformous mites) and Isopoda (Nicolai 1986, Büchs 1988). The various microhabitats (e.g., cryptogam species or crevices) used by these trunk-dwelling arthropods fundamentally modify the abiotic and nutritional living conditions (e.g., Gerson and Seaward 1977, Prinzing and Wirtz 1997). The arthropods make many decisions regarding microhabitat use throughout a day. For instance, many arthropods change microhabitat as soon as the surrounding area (e.g., square centimeter) of bark heats up (Prinzing 1997, 2001, Prinzing and Wirtz 1997). The selection
of oviposition sites requires further long-term decisions on microhabitat use (Prinzing 1996). Given all these decision processes, optimal-foraging theory may be useful to explain why some trunk-dwelling arthropod species are specialists in terms of microhabitat use, while other species on the same trunks are generalists. Specifically, the Time-Limited Disperser Model may be applicable, given that the arthropod species differ fundamentally in each of the above-mentioned traits that control search time. The species differ in their residency on the trunks, their speed of movement, and their tolerance of abiotic harshness (esp. frequent desiccation on exposed trunk surfaces, Table 1). The species also differ drastically in generation time, reflected in differences in oviposition periods (which, however, are known only for some of the arthropod species on trunks) (e.g., Jentsch 1940, Wunderle 1992). Hence, in the present study, I tested whether the degree of microhabitat specialization of species increases with increases in their residency, tolerance of desiccation, speed of movement, and generation time.

**METHODS**

**Study sites**

The investigations were conducted in five rural areas in northern Germany (details in Prinzing 1997) from August 1993 through April 1994. During this time of year, the bark microhabitats are colonized by the largest diversity of arthropods (Nicolai 1985, Büchs 1988). I

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<table>
<thead>
<tr>
<th>Traits, categories, and definitions</th>
<th>Sources (see footnotes)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Residency on exposed trunks during the period of investigation</strong></td>
<td>1, 3, 5, 6, 8, 9, 10, 11, 13, 17, 18, 19, 23, 28, 29, 30, 31, 34, 37, 39, 41, 42, 43, 44, 45</td>
</tr>
<tr>
<td>(1) Low. Each of the following criteria was fulfilled: Animals did not reproduce on the trunks. The trunks were colonized for much less than a life span (at most for 5 mo/yr). Abundances at the trunk fluctuated by &gt;50% between day and night, as well as between different weather conditions (sunny vs. cloudy, or cloudy vs. rainy weather).</td>
<td></td>
</tr>
<tr>
<td>(2) Moderate. Each of the following criteria was fulfilled: Animals reproduce frequently on trunks as well as in the litter between the trunks. The trunks were colonized for &gt;5 mo/yr, but with a wave-like pattern (i.e., significant increase and subsequent decrease throughout this time). Abundances at the trunk fluctuated by more than 50% during day and night, as well as between either sunny and cloudy, or cloudy and rainy weather.</td>
<td></td>
</tr>
<tr>
<td>(3) High. Each of the following criteria was fulfilled: Animals reproduce frequently on trunks, but rarely in the litter between the trunks. The trunks were colonized for &gt;6 mo, without displaying a wave-like pattern. Abundances at the trunk fluctuated by less than 50% either between different weather conditions, or between day and night.</td>
<td></td>
</tr>
<tr>
<td>(4) Almost complete. Each of the following criteria was fulfilled: Animals did reproduce on the trunks and can only reproduce on tree bark, not in the litter. The trunks were colonized for &gt;6 mo, with an increase in abundances during the species’ hatching period, and a decrease prior to the species’ diapause. Abundances at the trunk fluctuated &lt;25% between day and night, or between different weather conditions</td>
<td></td>
</tr>
<tr>
<td><strong>Tolerance of desiccation</strong></td>
<td></td>
</tr>
<tr>
<td>(1) Exposure to unsaturated atmosphere is tolerated for 1 or a few hours.</td>
<td>16, 21, 22, 29, 32, 33, 35, 43, 44</td>
</tr>
<tr>
<td>(2) …for 1 or 2 days.</td>
<td></td>
</tr>
<tr>
<td>(3) …for several days.</td>
<td></td>
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<tr>
<td>(4) …for several days combined with the capability to move freely on sun-exposed bark.</td>
<td></td>
</tr>
<tr>
<td><strong>Speed of movement (by walking)</strong></td>
<td>8, 39, 44</td>
</tr>
<tr>
<td>(1) Approximately &lt;0.15 cm/s; (2) 0.15 to &lt;0.5 cm/s; (3) 0.5—&lt;1.5 cm/s; (4) ≥1.5 cm/s.</td>
<td></td>
</tr>
<tr>
<td><strong>Length of generation</strong></td>
<td>2, 5, 12, 18, 22, 24, 25, 26, 27, 29, 30, 36, 39, 44</td>
</tr>
<tr>
<td>(1) Time span from hatching until most eggs are laid &lt;3 months; (2) 3 months—&lt;1 year; (3) mostly ≥1 year.</td>
<td></td>
</tr>
</tbody>
</table>

Notes: Key to sources: (1) Allmen and Zettel (1982); (2) Altmüller (1979); (3) Beck and Woas (1991); (4) Belfido (1979) for a closely related species; (5) Büchs (1988); (6) Cassagnau (1965); (7) Chvála (1975); (8) Chvála (1975) and Nicolai (1985, 1986) observe fast vertical movements of Tachypsea nubila on trunks, extending beyond the trunk heights considered in the present study; (9) database of “Forschungsstelle für Ökosystemforschung,” University of Kiel, Germany; (10) Den Boer (1961); (11) Ellis (1974); (12) Jentsch (1940); (13) Gisin (1943); (14) Gisin (1960); (15) Gruner (1965/1966); (16) Gunn (1937); (17) Günther (1974); (18) Heimer and Nentwig (1991); (19) U. Irmler, personal communication; (20) Joosse (1970); (21) Joosse and Veltkamp (1970); (22) Klima (1954); (23) Luxton (1981a) on a species very closely related to X. discrepans (X. tegeocranus); (25) Luxton (1981b) on X. tegeocranus [see note (24)]; (26) Heeley (1941), Meinertz (1949), and Zimmer and Kautz (1997); (27) Mertens and Blanquaert (1980); (28) Michoka (1987); (29) Nicolai (1985); (30) Péricart (1972); (31) Ponge (1993); (32) inferred from the habitat use, which is similar to O. cineta and slightly less extreme than E. nivalis (Cassagnau 1965; Ponge 1993); (33) Riha (1951); (34) Reinke and Irmler (1994) for the investigated part of Germany; (35) Rudolph (1982); (36) Schneider (1955); (37) Vegt (1987); (38) G. Weigmann, personal communication; (39) Wunderle (1992); (40) Willmann (1951); (41) Prinzing (1996); (42) Prinzing (1997); (43) Prinzing and Wirtz (1997); (44) A. Prinzing, personal observations; (45) predominantly nocturnal distribution in the present study (χ² = 7.4, P < 0.001, N = 34 animals). |
sampled a total of 299 tree trunks including the following species: *Quercus robur* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., and *Tilia* spp. (mainly *platyphyllos* Scop.). The trunks grew along small roads or field-paths or in meadows and were thus exposed directly to wind, sun, and precipitation. I included only trees with large trunks (≥2.5 m circumference at a height of 1.5 m), and sampled the area on these trunks between 0.8 and 1.8 m above the ground.

**Sampling**

I sampled the arthropods during different ambient conditions because many of the arthropod species use different microhabitats during different weather conditions (Prinzing 1997). For instance, I sampled 80 of the trunks at night, and I sampled during any weather condition I encountered. On each trunk, I separately sampled the different microclimatic zones, defining them according to the exposure to wind, sun, and precipitation at the moment of investigation (details in Prinzing 2001). Depending on ambient weather conditions, four to 10 microclimatic zones could be defined per trunk.

Within each microclimatic zone, I sampled the animals in the microhabitat types present. I searched for the animals focally (Mayer 1957, Bauer 1979, Prinzing 1997) in plots of defined surface area. The surface area is the dimension of a microhabitat that is most relevant to the animals because they graze on crusts on the trunk’s surface or on thin layers below it, or prey upon the surface-dwelling grazers (Mayer 1957, Prinzing and Wirtz 1997). First, I searched the crustose microhabitat types with a 7×-magnification distance lens from 60 cm away. I searched composite plots, each covering 10 fields-of-view of microhabitat surface (10 × 3.1 cm²). Then, I searched all microhabitat types with a 10×-magnification hand lens. Again, each plot covered ten fields-of-view of microhabitat surface (10 × 1.8 cm²). I selected the fields-of-view with a grid. All grid cells were sampled, and samples were placed haphazardly within grid cells (Krebs 1999). During these hand-lens searches, I examined the inner surfaces of cavities according to the following procedure (Prinzing 1997): (a) I illuminated dark cavities of radial crevices and of *Evernia prunastri* thalli with a pen light. (b) I searched radial crevices over a length that, multiplied by the approximate depth of the crevices, equaled 18 cm². If a radial crevice was difficult to survey by eye, I examined it in addition while gently scraping with a large needle. This did not bring any additional animals to light. (c) I opened thalli of *Evernia prunastri* in several layers with a large needle. (d) I scraped off crustose microhabitats, after I examined their surface, to sample mining *Carabodes labyrinthicus* (Oribatei). (e) Finally, I broke up the vertical crevices with a knife.

I recorded all macroscopic arthropods. I could identify most of the Collembola, Psocoptera, Isopoda, and Heteroptera in the field; I identified other animals in the laboratory. Identification and nomenclature followed Gisin (1960) for Collembola; Günther (1974) for Psocoptera; Péricart (1972) for Heteroptera; Chvála (1975) for Diptera; Roberts (1984) and Heimer and Nentwig (1991) for Araneae; Sellnick and Forsslund (1952) and Beck and Woas (1991) for oribatid mites; Michoka (1987) for trombidiformous mites; and Gruener (1965/1966) for Isopoda. I refer to *Bdella semiscuta*
Table 2. Sample size, traits, and microhabitat-niche breadths of species.

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Resid</th>
<th>Des</th>
<th>Speed</th>
<th>Gener</th>
<th>Niche breadth</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Collembola</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Orchesella cincta</em></td>
<td>328</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>0.74</td>
</tr>
<tr>
<td><em>Entomobrya nivalis</em></td>
<td>320</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>0.52</td>
</tr>
<tr>
<td><em>Entomobrya albocincta</em></td>
<td>439</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1.08</td>
</tr>
<tr>
<td><strong>Psocoptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cerobasis guestifalica</em></td>
<td>398</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1.14</td>
</tr>
<tr>
<td><em>Reuterella helvimacula</em></td>
<td>70</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>1.47</td>
</tr>
<tr>
<td><strong>Heteroptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Loricula elegans</em></td>
<td>37</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>1.75</td>
</tr>
<tr>
<td><em>Temnostethus gracilis</em></td>
<td>30</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>1.88</td>
</tr>
<tr>
<td><strong>Diptera</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Tachypeza nabila</em></td>
<td>34</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>2</td>
<td>1.07</td>
</tr>
<tr>
<td><strong>Isopoda</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Porcellio scaber</em></td>
<td>489</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1.32</td>
</tr>
<tr>
<td><strong>Oribatid Acari</strong></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>Carabodes labyrinthicus</em></td>
<td>224</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>1.02</td>
</tr>
<tr>
<td><em>Xenillus discrepans</em></td>
<td>54</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>2.07</td>
</tr>
<tr>
<td><strong>Trombidiformous Acari</strong></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bdella cf. semiscuta</em></td>
<td>53</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>1.54</td>
</tr>
<tr>
<td><strong>Araneae</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>Entelecara penicillata</em></td>
<td>83</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>0.76</td>
</tr>
<tr>
<td><em>Lathys humilis</em></td>
<td>29</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>0.76</td>
</tr>
</tbody>
</table>

Notes: N = number of animals sampled. Trait categories are defined in Table 1. Abbreviations are: Gener, length of generation; Resid, residency on the trunk; Des, tolerance of desiccation; Niche breadth, microhabitat-niche breadth quantified as Simpson index. Species are given in taxonomic order.

as “cf.” (Table 2) because the description of this species needs revision (S. Swift, personal communication).

To calculate the abundances of Heteroptera and Diptera on crustose microhabitats, I used data only from the distance-lens searches (Table 2) because these animals showed flight behavior during hand-lens searches, which caused lower abundances to be recorded. For the remaining species, I generally used data from the hand-lens searches. I evaluated distance-lens searches only in the rare event that a species was found with the distance lens, but not with the hand lens (<1% of the plots). In that case, the species might have been chased away during the hand-lens search. To further assess if there was any collection bias associated with hand-lens searching, I tested many animals that had been spotted from a distance by approaching them directly with the hand lens (N ≥ 10 animals per species). This did not induce flight behavior, except in the above-mentioned Heteroptera and Diptera. Moreover, after searching the bark with the hand lens in the field, I found no additional animals by dissecting the bark with a large needle under the stereomicroscope (total 10 samples were investigated this way).

I recorded juvenile and adult *Carabodes labyrinthicus* (Oribatei) separately because their very distinct morphologies may correspond to differences in micro-habitat use and specialization (Klima 1954, MacNally 1995). However, it turned out that both stages were very similar in their microhabitat specialization (Fig. 2) and identical in the biological traits considered (Table 2). Therefore, in the following analysis, I assigned *C. labyrinthicus* to the mean between the two stages to avoid “pseudoreplication” within species.

Analysis

I assigned each species to four traits: residency, tolerance of desiccation, speed of movement, and length of generation (Table 1 shows trait definitions; Table 2 shows assignments of species). The traits I considered are all inherently continuous. Desiccation tolerance, for instance, may take any possible degree in between the extremes. In the analysis, however, the available information did not permit me to score the species continuously along these trait axes. Rather, I had to divide the trait axes into distinct categories and assign the species traits to these categories. I chose the categories in a way that they reflected the full range of trait values realized in the species community investigated. The exact definition of trait categories, however, was largely dictated by the available knowledge. Speed of movement, for instance, was not known at a scale of millimeters per second, and hence it was not possible to define the categories at such a
Fine scale. However, even such coarse-scale ordinal categorical variables are generally amenable for multiple regression analyses (Jongman et al. 1987). Moreover, in the analysis across phylogenetically independent contrasts as data points, the categories tend to disappear. The reason is that many contrasts are differences between ancestral states which often have values in between the ordinal categorical values of the
extant species. Therefore, contrasts are much more continuously distributed than the original ordinal categories of species.

I defined the microhabitat-niche breadth as the diversity of microhabitat types utilized by a species (Krebs 1999). I used the log, transformed Simpsons index for finite populations (SI; Rosenzweig 1995). Because some microhabitat types were more frequent than others, I first calculated the mean abundances of species in each microhabitat type and then used these abundances to calculate SI. Hence, my measure of microhabitat-niche breadth was independent of frequency, or availability, of microhabitats (Krebs 1999). Among the indices that take into account the variation of abundances across microhabitats, SI is generally the least biased (Rosenzweig 1995, Mouillot and Lepêtre 1999). Also, I found that SI was independent of sample size (Pearson correlation was not statistically significant at P > 0.2). Another robust index of niche breadth is Fisher’s alpha (FA; Rosenzweig 1995). However, FA does not take into account the variation of abundances across microhabitats. Moreover, FA requires a drastic adjustment when several species utilize all microhabitat types (Rosenzweig 1995). In the present study, I found that analyses based on FA led, qualitatively, to the same results as analyses based on SI, so I present only the latter.

For practical and for conceptual reasons, I included all microhabitat types in the analysis. A practical reason was that I could not see any physical limitation, such as cavity size or surface structures, that could fully prevent any of the species from using any of the microhabitat types (personal observations and references given in Table 1). Even though the field counts seemed to indicate that some species never used certain types of microhabitats (Fig. 2), such a conclusion would be premature. The conclusion would very much depend on the sample size. The smaller the sample of a given species, the more likely it is that the species will never appear in certain microhabitat types. Although the species do differ in the efficiency by which they use a given microhabitat type, this efficiency cannot be quantified in a straightforward and comprehensive way and is therefore a poor guide to decide which microhabitat types to include in a niche-breath measure. The topic is further complicated by the fact that species seem to differ in the efficiency by which they use different microhabitats (see Fig. 2; personal observation). A conceptual reason for including all microhabitat types was that the definition of niche breadth is based solely on the resource (food, microhabitat, etc.) use of a given species, and does not consider whether coexisting species are able to use the same resource types (Begon et al. 1990).

I investigated the relationship between the microhabitat-niche breadth of species and their residency on the trunks, tolerance of desiccation, speed of movement, and length of generation, using multiple regression analysis. Given that my objective was to assess the relative importance of all independent variables, rather than reduce the number of variables, I included all variables at once. I calculated two versions of the analysis. In one version, I used species as data points; in the other, I used phylogenetically independent contrasts (Felsenstein 1985). Such contrasts are standardized differences between sister taxa. The use of contrasts, rather than species, as data points reduces the problem of phylogenetic non-independence among species (Harvey and Pagel 1991; for patterns of specialization, see Jermy 1998). Moreover, the use of contrasts eliminates the effects of the hidden phylogenetic correlation between the traits that are being studied and other traits (Burt 1989, Brown 1995). Theoretically, the calculation of contrasts requires information on phylogenetic branch lengths, which was not available for the arthropods investigated. However, simulations (e.g., Martins and Garland 1991), and empirical studies (e.g., Blackburn et al. 1996, Ackerly 2000, Dunn et al. 2001; personal observations) demonstrate that it is valid to calculate contrasts even when branch lengths are arbitrarily set to one. Thus, I set all branch lengths to one. Analyses of contrasts are based on assumptions of phylogenetic independence as well as homoscedasticity. I tested both assumptions according to Freckleton (2000) and Garland et al. (1992), and log, transformed residency-contrasts to meet the assumption of homoscedasticity (Garland et al. 1992). Regressions of contrasts were forced through the origin (Harvey and Pagel 1991), which only minimally changed the statistical results (i.e., P values changed by <0.04).

Finally, I explored the results of my final, phylogenetically corrected analysis in several ways to make sure that they were sufficiently robust. Concerns over robustness stemmed from the small sample size and the comparatively large number of independent variables used in my analyses. Also, the categorization of inherently continuous traits inevitably introduced random error into the analysis, which can distort results when the sample size is small. (Systematic error was not an issue, given that I had defined the categories, and assigned the species, prior to the analysis.) First, I explored whether the results were biased by multicollinearity among independent variables. To this end, I calculated the tolerance for each variable, i.e., the variance of a variable that was not explained by other independent variables (StatSoft 1999). Large tolerance indicates low multicollinearity. Second, I explored whether the test results were biased by violations of the normality assumption; I compared the t values to a null expectation from a randomization (N = 10000; based on REGRESSN [P. Legendre, unpublished program]). Results of this randomization test were nearly identical whether the observations or the residuals were randomized. Third, I explored whether the results were stable when I changed the absolute values of contrasts. For this purpose, I set all contrasts to the same absolute
value: positive contrasts = +1, negative contrasts = −1. I summed these contrasts across those variables that had been identified as significant predictors of microhabitat-niche breadth in the original analysis (see Results). Then, I tested whether the sum was positive when the niche-breadth contrast was positive, and negative when the niche-breadth contrast was negative, using a one-tailed Fisher test (Sokal and Rohlf 1994).

Fourth, I explored whether the results were biased by outliers. I omitted one data point at a time, reanalyzed the remaining 12 data points, and compared the results with those of the original analysis. Fifth, I used bootstrap resampling (N = 10,000) to estimate the credibility of the regression parameters, i.e., to estimate what can be expected from further sampling the population (Manly 1991). I resampled the observations, rather than the residuals, as recommended for small sample sizes and for nonmanipulative observational studies (Simon 1990–1999, Manly 1991, personal communication). The choice of procedure, however, does not seem to be crucial (Manly 1991).

Analyses were conducted using the programs COM-PARE (E. P. Martins, unpublished program [COM-PARE 2.0]). SYSTAT (Wilkinson 1992), REGRESSN (P. Legendre, unpublished program), and RESAMPLING STATS (Simon 1990–1999). All P values presented in the Results section are from one-tailed tests.

Results

In total, 14 species were found on the trunks during at least two months. These species included Collembola, Psocoptera, Heteroptera, Diptera, Araneae, orbibatid mites, trombidiformous mites, and Isopoda (Table 2) and are all known to be bark-dwellers (Nicolai 1985, Büchs 1988). The degree of microhabitat specialization varied greatly among these species. The most specialized species was the collemboian Entomobrya nivalis. In its most densely colonized microhabitat type, E. nivalis reached an abundance that was 6.1 times as great as the mean abundance across all microhabitat types (Fig. 2). The Simpson index of X. discrepans was 2.07 (Table 2). Differences in the microhabitat specialization among arthropod species were not correlated with their distribution across tree species. For instance, most arthropod species were most abundant on either Tilia spp. or Fagus sylvatica. But the arthropod species that were most abundant on Tilia spp. and those most abundant on Fagus sylvatica did not differ significantly in their microhabitat specialization (ANOVA: N = 10 species; F1,8 = 1.89; P = 0.21).

When I used species as data points to analyze the relationship between the degree of microhabitat specialization and traits that control search time, the results supported three of the four predictions of the Time-Limited Disperser Model: specialists (i.e., species with a small niche breadth) were resident on the trunks, could move fast, and had a long generation time (Table 3). However, contrary to model predictions, specialists were sensitive to desiccation. When I used phylogenetically independent contrasts as data points, I found similar results, except that specialists turned out to be even more resident on the trunks and were less sensitive to desiccation (Table 3).

When I tested the robustness of the final, phylogenetically corrected analysis, I found, first, that the multicollinearity was low: tolerance values of independent variables always exceeded 0.43. Second, the error probabilities changed less than 0.005 when I applied a randomization test. Third, the results were only minimally affected by the absolute values of the contrasts. When I set all contrasts to the same absolute value of one, I found that the sum across the three relevant variables, residency, speed of movement, and generation time, was generally positive when the niche-breadth contrast was also positive; the sign was negative when the niche-breadth contrast was negative (one exception; N = 10 contrasts; Fisher test; P = 0.024). Fourth, the results were only slightly biased by outliers. Omitting individual data points hardly changed the results. The sign of the partial regression coefficients never changed. Traits that had been significant (P < 0.05) in the original analysis remained significant in 32 out of 39 cases, or marginally significant (P < 0.1) in another five cases. Only the effect of generation time was not

<table>
<thead>
<tr>
<th>Trait</th>
<th>Species (R2 = 0.73)</th>
<th>Contrasts (R2 = 0.54)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Beta</td>
<td>P</td>
</tr>
<tr>
<td>Residency on trunk</td>
<td>−0.38</td>
<td>0.005</td>
</tr>
<tr>
<td>Tolerance of desiccation</td>
<td>0.67</td>
<td>&gt;0.5</td>
</tr>
<tr>
<td>Speed of movement</td>
<td>−0.76</td>
<td>0.007</td>
</tr>
<tr>
<td>Length of generation</td>
<td>−0.58</td>
<td>0.015</td>
</tr>
</tbody>
</table>

Notes: Results of multiple linear regression analyses. Data points are either species (N = 14) or phylogenetically independent contrasts (N = 13). Beta = standard regression coefficient; P = error probability.
statistically significant (0.1 < *P* < 0.15) in two cases. Fifth, I found that in the analysis of bootstrapped samples, 98.8% of the estimates of the regression parameter of residency on trunks were negative, just as in the analysis of the original sample. The corresponding values for tolerance of desiccation, speed of movement, and length of generation were 98.3%, 97.6%, and 93.4%, respectively. This result strengthened the conclusions from my original analysis concerning residency on trunks, tolerance of desiccation, speed of movement, and to some degree also concerning length of generation.

**Discussion**

In the present study, I investigated the arthropod species that coexist on trunks of trees within a small region. I found that the species differed greatly in their degree of microhabitat specialization (Table 2). These differences were clearly related to life history (Table 3). Specialists were resident on the trunks for much of their lives and had a long generation time. Thus, specialists spent more time on the trunks than generalists. Moreover, specialists could move fast and could thus cover a given search distance more promptly than could generalists. Overall, specialists were less limited with respect to search time than generalists, both at a daily scale and at a lifetime scale. These findings confirmed three predictions of the Time-Limited Disperser Model. One prediction, though, was not confirmed: specialists proved no more tolerant of desiccation than were generalists. Thus, specialists could not extend their search into periods of dry weather.

The results of the present study are specific to the scale of my study. I considered a tiny geographic area extending over <750 km². In contrast, other studies have considered much larger areas. Across larger areas, the range size of species may play an important role in determining their resource specialization. Species that occupy a small range may encounter only limited types of resources, and thus be more specialized than wide-ranging species (Jaenike 1990). In the present, small-scale study, however, species range was not a concern. All types of microhabitats were present throughout the complete area of investigation.

The evidence presented is only correlative, a limitation inherent in comparative analyses across a number of species. It is simply not possible to experimentally manipulate the traits of the species in the field. Given the uncertainty associated with correlative evidence, it is important to consider whether the results could also be explained by factors other than search-time limitations. Such factors include physiological or morphological constraints on the ability of specialists to efficiently use a larger number of microhabitats, or to efficiently use certain types of microhabitats. First, specialists might have been incapable of efficiently perceiving additional microhabitat types (Bernays 2001). However, if this were the case, oribatid mites should have been much more specialized since they are blind and perceive substrate humidity only slowly, except when surrounded by the substrate (Riha 1951). Collembo and the fly *T. nubila*, in contrast, should have been much more generalized in microhabitat use, as these species have high perception capabilities (Hopkin 1997, Jacobs et al. 1998). Second, specialists might have been incapable of withstanding the microclimates of certain microhabitat types, in particular the desiccation at the surface of crustose cryptogams (Southwood 1972, Prinzing and Wirtz 1997). A correlation between specialization and susceptibility to desiccation does, indeed, support this possibility. However, this correlation was only weak and there are many counter-examples. For instance, the species with the lowest desiccation tolerance, *P. scaber*, was rather generalized in microhabitat use (Table 2). Third, specialists might have been incapable of finding the rare microhabitat types (Howe and Westley 1988). However, if this were the case, specialists should have been restricted to algal crusts and radial crevices, the two most abundant microhabitat types. Fourth, specialists might have been incapable of efficiently metabolizing many food types owing to an adaptation to just a few toxic food types (Jaenike 1990). However, if this were true, specialists should have been restricted to *P. albescens* and *L. ex-
of the important candidates to explain patterns of microhabitat specialization, even among species.

In conclusion, my observations support the Time-Limited Disperser Model at an interspecific level. Species with few constraints on their search time can afford to be choosy. Animals that are more limited in search time, in contrast, often have to accept suboptimal choices and are thus more generalized. This finding has three general implications. First, it implies that resource specialization of species may be explained by their resource-use behavior. This explanation is contrary to classical explanations, which invoke morphological, physiological, or phylogenetic constraints (discussed above). Second, it implies that specialization may be evolutionarily flexible. It depends on evolutionary changeable traits, such as generation time or residency—traits that can vary greatly within a given genus (Gisin 1960, Péricart 1972, Günther 1974, Prinzinger 1996). Indeed, other authors have previously pointed to the evolutionary flexibility of specialization (e.g., Kelly and Farrell 1998, Janz et al. 2001). But the notion of specialization as an inflexible property, an “evolutionary dead end,” still has many advocates among paleontologists and biogeographers (Kammer et al. 1997, Ricklefs and Miller 2000). Third, it implies that there are proximate benefits in being specialized, given that animals with a search-time budget that permits specialization indeed do specialize. One benefit might be the very consistent environment in which specialists live (Kawecki 1998). Another benefit might be the restricted and thus more manageable amount of information to which specialists are exposed (Bernays 2001). Until now, such benefits of specialization have rarely been considered to explain why some species in a given environment are more specialized than others.

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Literature Cited


