

MOVEMENT PATTERNS OF RATS AND TREESHREWS IN BORNEAN RAINFOREST INFERRED FROM MARK- RECAPTURE DATA

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Abstract. Movement and space-use patterns influence animal population dynamics and interactions with the environment in various ways. In this study, we estimated movement patterns of six rat (Muridae) and four treeshrew (Tupaiaidae) species from Borneo based on mark-recapture data in three unlogged and three logged rainforest sites. The treeshrews *Tupaia gracilis*, *T. longipes*, and *T. tana* moved longer straight-line distances than any of the observed rats, with the largest movement distances recorded for *T. longipes*. The largest mean movement distance for rats was observed for the giant rat *Leopoldamys sabanus*, while the shortest movements were recorded for the rats *Maxomys whiteheadi* and *Sundamys muelleri*. Generally, rats showed a higher frequency of short movements than treeshrews, suggesting that rats are more restricted in their ranging patterns compared with the more exploratory movements of treeshrews. Mixed effects modeling suggests a significant impact of forest type on movement patterns of *L. sabanus*, and marginal impacts on the movements of *N. cremoriventer* and *T. longipes*. Significant sex- and age-specific effects were detected for *L. sabanus*, *N. cremoriventer*, *M. surifer*, *M. whiteheadi*, *S. muelleri*, *T. longipes*, and *T. gracilis*. Interacting effects such as forest age and type on movements of *L. sabanus*, as well as the relatively weak effect of forest type in mixed-effects analysis for *T. tana*, in contrast to univariate analysis, indicate that various factors appear to simultaneously influence movements. While trapping data allow a first insight into how species of rats and treeshrews differ in using the rainforest environment, more detailed and specific investigations are needed to understand space-use patterns. Accepted 26 November 2008.

Key words: Borneo, Muridae, recapture, spatial use, Tupaiaidae.

INTRODUCTION

Movement and space-use patterns have profound effects on spatially structured populations, habitat colonization, and the consequent interactions with the environment. The spatial scale of food consumption, dispersal of nutrients and seeds via feces, and exposure as prey and as host to other organisms are processes affected by spacing behavior (Brown *et al.* 1994, Boyer *et al.* 2006, Morales & Carlo 2006). Knowledge of species-specific differences in space-use patterns within species-rich small mammal assemblages is therefore needed to distinguish species population structures and basic ecology. However, movement and ranging patterns are generally difficult to study and remain poorly known for mammals in tropical forests. With only a handful of small mammal species in SE Asian forests having been investigated in terms of their movement (Kawamichi

& Kawamichi 1979, Emmons 2000, Wells *et al.* 2006b, Munshi-South *et al.* 2007, Wells *et al.* 2008), a basic idea of how movement patterns might help to understand the occurrence and coexistence of small mammals in species-rich assemblages in these forests is lacking. Most often, the concept of home ranges, described as the area most frequently used by an animal, has been considered as a measure for animal space use (Aebischer *et al.* 1993, Gautestad & Mysterud 1995). Alternatively, the order of straight-line distances inferred from mark-recapture studies provides simultaneous information on a larger range of species in an assemblage. Although such a distance measure comprises a relatively rough approximation of movement patterns, it has been postulated as co-varying with home range sizes (Slade & Russell 1998, Bowman *et al.* 2002). Moreover, the comparative characteristic of movement distances measured simultaneously for several species may eventually allow comparisons on various scales, from intraspecific traits to assemblages from different

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study sites, that may advance our knowledge on how movement patterns vary across species, habitats, or other scales of analysis. So far, movement distances have been recorded for various Neotropical small mammal assemblages (Gentile & Cerqueira 1995, Pires *et al.* 2002, Püttker *et al.* 2006).

Borneo is considered a hotspot of biodiversity with a high level of endemism (Myers *et al.* 2000) and a rapid loss of the remaining natural forest (Curran *et al.* 2004). Yet compared with other organisms, small mammals remain little investigated, and data on movement distances for most species are not available. Rats and treeshrews comprise two of the most species-rich components of the non-volant small mammal assemblages, with species of both groups utilizing various habitats from the ground to the canopy (Bernard 2004, Wells *et al.* 2006a,b).

As a result of a trapping study over two years with repeated sampling in different forest sites (Wells *et al.* 2007), we obtained a reasonable sample size of movement distances to estimate differences in movement patterns within a small mammal assemblage from Borneo.

METHODS

Study area and animal capture. This study took place in the lowland rainforest in Sabah (Malaysia) in northern Borneo in three protected unlogged rainforests at Danum Valley Conservation Area (4°57'N, 117°48'E), Poring in Kinabalu National Park (6°02'N, 116°42'E), and Tawau Hills National Park (4°23'N, 117°53'E), as well as three logged forests at Luasong Field Center (4°36'N, 117°23'E), Kampong Monggis (6°13'N, 116°45'E), and Kampong Tumbalang (6°08'N, 116°53'E). All of these forests comprised more than 1000 hectares; they were between 17 and 236 km apart and situated at altitudes of 200–900 m. Details of the logging histories at the various sites were not available, but all logged sites were structurally similar. Harvesting of commercially valuable trees such as dipterocarps 25–35 years previous to our study resulted in reduced canopy heights and denser undergrowths. At each forest site we established a randomly located and permanently marked transect of 40 trap stations equally spaced 20 m apart in two parallel lines on the forest floor. Animals were captured with locally made wire-mesh live traps (280 mm × 140 mm × 140 mm) between September 2002 and November 2004. We conducted 18 trapping sessions, alternating between six study sites with a mean interval of 103 ± 50 days between consecu-

tive trapping sessions at the same forest site. The traps were baited with banana and checked every morning for 16 consecutive days during each trapping session. All first captures were marked with a subcutaneously placed pit tag (ARE 162 transponders, AEG), measured, sexed, and aged based on the pelage and then released at the point of capture. As it was not always possible to determine the sex of immatures, some were classified as “unspecified” with regard to sex. Further details of the trapping survey are given in Wells *et al.* (2007).

Data analysis. We analyzed movement distances inferred from transect trapping data for all individuals of the most commonly-caught species, for which at least two captures within a trapping session allowed the calculation of distances moved between two successive captures (CD). Inter-trap distances from individual movements revealed considerable variation in distances moved between successive captures for all individuals and species as estimated by the coefficient of variation $CV = (S.D./mean) * 100$ (averaged CVs ranged from 50.8 ± 25.4 for *Tupaia gracilis* to 94.1 ± 49.5 for *Sundamys muelleri*), and we considered all specific movement distances as a representative data set rather than averaging across individuals. Considering individuals and time between captures as random effects in a generalized mixed effects model enabled us to allow for non-independence of movement distances and to consider individual-level variation as an informative trait during analysis. The time between consecutive captures pooled across all species ranged from 1 to 14 days, averaging 2.0 ± 1.8 days.

To test for the effects of forest type, sex, and age of individuals on movement distances of different species, we used generalized linear mixed effects models (GLMM) fitted by Laplace approximation, assuming a quasi-Poisson distribution due to overdispersion in the data (Pinheiro & Bates 2000), as implemented in the ‘lme 4’-package (Bates *et al.* 2008, R Development Core Team 2008). For these analyses, we fitted forest type, sex, and age as fixed effects, while individuals nested within the different study sites and time between captures were considered as random effects.

We fitted separate models for individual species and, additionally, used an equivalent GLMM with the data from all species combined, and species or taxonomic groups as fixed effects, to test for overall differences in movement distances. The significance

of fixed effects in these models was tested with likelihood ratio tests. For pair-wise comparisons, we used Mann-Whitney U tests and Kolmogorov-Smirnov tests with corrections for multiple testing as suggested by Benjamini & Hochberg (1995). Note that these tests were used, despite their limitations in considering grouping structures or random effects, because multiple comparison post-hoc tests were not yet fully implemented for quasi-Poisson GLMMs at the time of analysis.

RESULTS

Interspecific variations in movement patterns. Mark-recapture data for a total of 221 individuals from six species of rats (Muridae) and four of treeshrews (Tupaiaidae) were included in analyses; all species were trapped in both logged and unlogged forest sites

with a total of 948 recorded movements between consecutive captures (Table 1).

The distances moved between consecutive captures (CD) differed significantly across these small mammal species, and there was a significant overall impact of sex and age, but not of forest type, on movement distances (GLMM, species: $\text{Chi}^2 = 25.0$, $P < 0.01$, sex: $\text{Chi}^2 = 654.0$, $P < 0.01$, age: $\text{Chi}^2 = 59.4$, $P < 0.01$, forest type: $\text{Chi}^2 = 2.7$, $P = 0.10$). Movement distances of treeshrews were overall significantly larger than for rats (GLMM, groups: $\text{Chi}^2 = 12.5$, $P < 0.01$).

Tupaia gracilis, *T. longipes*, and *T. tana* showed significantly larger movement distances than any of the observed rat species (all Mann-Whitney U-tests adjusted $P < 0.05$). The largest movement distances observed were for *T. longipes*, with a mean CD of 72 ± 65 m. The largest CD during the study was

TABLE 1. Studied species, their body mass, the numbers of individuals recaptured, and the numbers of movement distances between consecutive captures in logged (LF) and unlogged (UF) forests, and mean distances between consecutive captures. Body masses of adults are given as the mean proportions of body mass with one S.D. of individuals captured as part of the entire trapping effort (see Wells *et al.* 2007).

Species	Family	Body mass [g]	Number of individuals recaptured	Number of CDs recorded UF/LF	Mean distance [m] between consecutive captures (CD)
Long-tailed giant rat <i>Leopoldamys sabanus</i>	Muridae	368 ± 64 (n = 101)	30	46 / 51	35 ± 30
Long-tailed tree rat <i>Niviventer cremoriventer</i>	Muridae	69 ± 13 (n = 142)	70	69 / 370	27 ± 32
Brown spiny rat <i>Maxomys rajah</i>	Muridae	160 ± 35 (n = 28)	16	46 / 28	27 ± 49
Red spiny rat <i>Maxomys surifer</i>	Muridae	157 ± 47 (n = 38)	12	4 / 41	22 ± 23
Whitehead's rat <i>Maxomys whiteheadi</i>	Muridae	53 ± 11 (n = 30)	9	34 / 10	21 ± 16
Muller's rat <i>Sundamys muelleri</i>	Muridae	204 ± 29 (n = 27)	11	8 / 36	21 ± 29
Slender treeshrew <i>Tupaia gracilis</i>	Tupaiaidae	81 ± 19 (n = 14)	6	15 / 3	60 ± 43
Common treeshrew <i>Tupaia longipes</i>	Tupaiaidae	196 ± 25 (n = 59)	20	50 / 3	72 ± 65
Lesser treeshrew <i>Tupaia minor</i>	Tupaiaidae	58 ± 9 (n = 31)	23	16 / 47	33 ± 28
Large treeshrew <i>Tupaia tana</i>	Tupaiaidae	218 ± 27 (n = 126)	24	23 / 48	49 ± 35

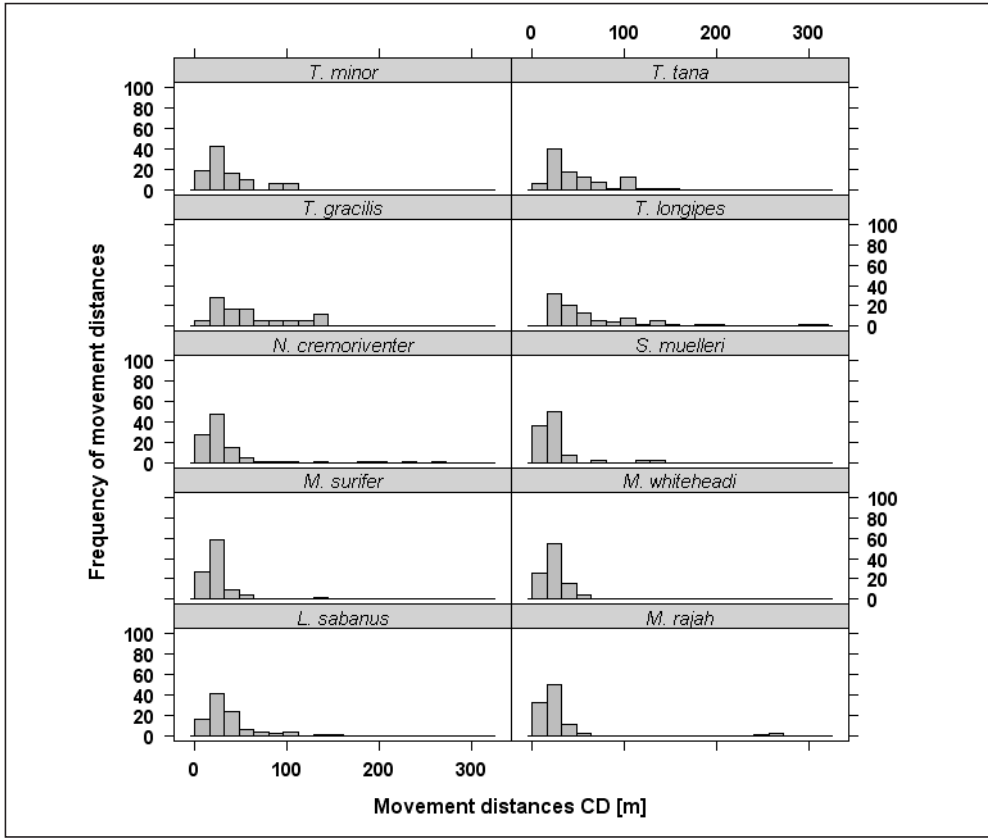


FIG. 1. Frequency distribution of movement distances between consecutive captures (CD) for commonly-caught species of treeshrews (*Tupaia minor*, *T. tana*, *T. gracilis*, *T. longipes*) and rats (*Niviventer cremoriventer*, *Sundamys muelleri*, *Maxomys whiteheadi*, *M. surifer*, *M. rajah*, *Leopoldamys sabanus*) from Borneo.

320 m, recorded for both the treeshrew *T. longipes* and the rat *Niviventer cremoriventer*. The treeshrew *T. minor* moved significantly shorter distances (CD) than any other treeshrew species (all Mann-Whitney U-tests adjusted $P < 0.05$).

The largest movement distance for rats was observed in *Leopoldamys sabanus* with a mean CD of 35 ± 30 m, significantly larger than any of the other observed rat species (all Mann-Whitney U-tests adjusted $P < 0.05$). The shortest mean CDs were recorded for the rats *Maxomys whiteheadi* and *Sundamys muelleri* (see Table 1). Overall, the frequency distributions of movement distances were significantly different in 16 out of 45 pair-wise comparisons across species by the two-sample Kolmogorov-Smirnov test (all $D > 0.16$, adjusted $P < 0.05$) with 81 %

(13 out of 16) of these distinct distribution patterns found between rats and treeshrews (Fig. 1). Rat species typically moved short distances, with 60 % of their movements not exceeding 20 m. In contrast, 65 % of treeshrew movements were longer than 20 m, with treeshrews seldom recaptured in the same trap (Fig. 2). There was no evident relationship between specific body mass of adults as given in Table 1 and mean movement distances (linear regression on a \log_{10} - \log_{10} scale: $F = 0.318$, $df = 1, 8$, $P = 0.59$).

In summary, interspecific movement patterns described by CD revealed significant differences between these small mammal species. In particular, movement patterns differed between treeshrew species with similar appearances and body masses, such as *T. longipes* versus *T. tana* and *T. gracilis* versus *T.*

minor, suggesting that each species has its unique movement patterns adapted to its particular environment and niche.

Intraspecific differences in movement patterns. Movement distances of *L. sabanus* were significantly influenced by forest type and age, with larger movements of adults in logged than in unlogged forests and smaller movements of immatures in logged than in unlogged forests (GLMM, forest: $P = 0.026$, age: $P = 0.002$; Table 2). Marginal effects of forest type on movement distances were suggested for *N. cremoriventer* and *T. longipes* by mixed effects models (see Table 2). A significantly higher overall frequency of short movements in logged versus unlogged forests for *T. tana* was indicated by a Kolmogorov-Smirnov

test ($D = 0.40$, $P = 0.015$), whereas a mixed effects model suggested only a weak influence of forest type on movement distances of *T. tana*. Effects of sex on movement distances were suggested for *M. surifer*, *M. whiteheadi*, *N. cremoriventer*, *S. muelleri*, and *T. longipes*, and of age on *N. cremoriventer*, *S. muelleri*, and *T. gracilis* (Table 2).

DISCUSSION

Overall, movements inferred from mark-recapture data provided evidence that mean movement distances, as well as the frequency distribution of short and long moves, differed across species. Movements revealed distinct patterns at the rats and treeshrews level. Treeshrews showed longer mean and maximum

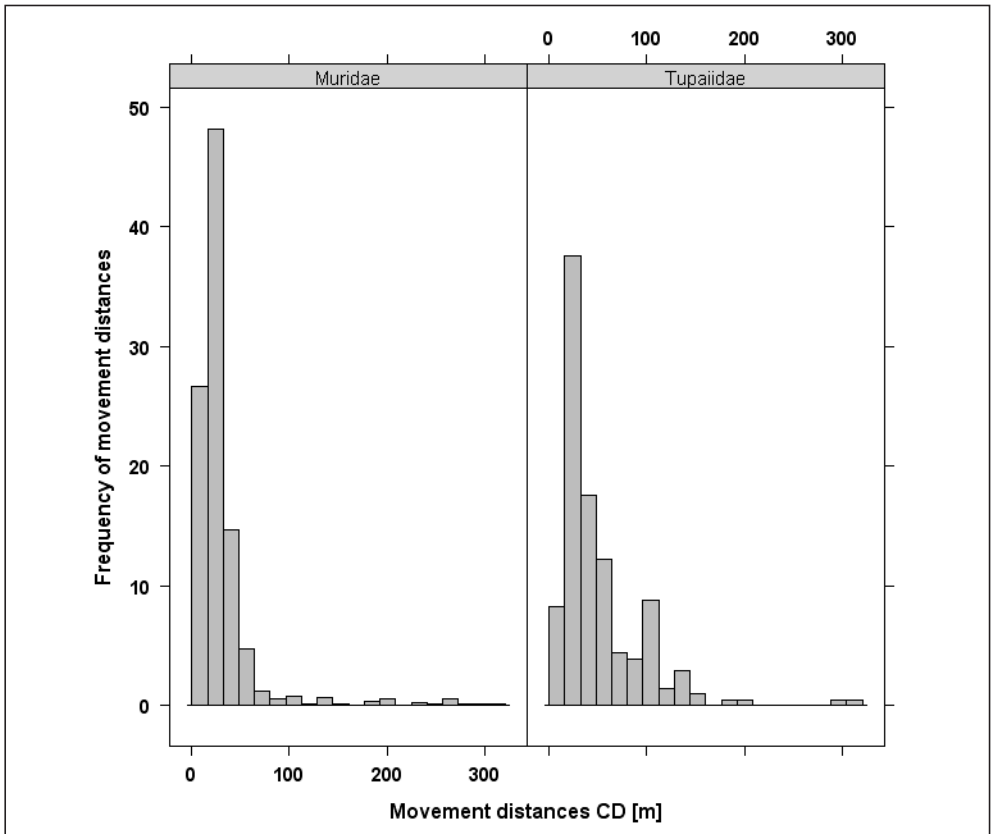


FIG. 2. Frequency distribution of movement distances between consecutive captures (CD) compared for rats (Muridae) and treeshrews (Tupaiaidae). Data are pooled for six species of rats and four species of treeshrews (see also Fig. 1).

TABLE 2. Impact of forest type, sex, and age on movement distances of various species as estimated by generalized mixed effects models. Significance of fixed effects are estimated by likelihood ratio tests, Chi² and P-values are shown with P < 0.05 in bold. Log-likelihood values and degrees of freedom are given for full specific models including all effects.

Species	Forest type	Sex	Age	Full Model (log-likelihood, D.F.)
<i>Leopoldamys sabanus</i>	0.026	0.6577	0.002	-700.8, df = 13
	4.9539	0.838	12.052	
<i>Niviventer cremoriventer</i>	0.052	< 0.001	< 0.001	-5585, df = 22
	3.7651	764.69	662.19	
<i>Maxomys rajah</i>	0.439	0.860	0.816	-911.5, df = 12
	0.6003	0.3008	0.0539	
<i>Maxomys surifer</i>	0.598	0.007	0.262	-223.6, df = 12
	0.2776	10.005	2.6764	
<i>Maxomys whiteheadi</i>	0.733	0.018	-	-288.2, df = 10
	0.0019	5.5429		
<i>Sundamys muelleri</i>	0.233	< 0.001	0.036	-268.4, df = 12
	1.422	13.915	4.4138	
<i>Tupaia gracilis</i>	0.371	-	0.008	-124.4, df = 11
	0.8017		9.6487	
<i>Tupaia longipes</i>	0.051	0.047	0.205	-308.5, df = 12
	3.807	6.1044	1.6062	
<i>Tupaia minor</i>	0.414	0.164	0.647	-536.3, df = 13
	0.6668	3.6124	0.8721	
<i>Tupaia tana</i>	0.221	0.758	0.802	-375.1, df = 12
	1.5001	0.5542	0.0631	

movement distances than rats, with a lower frequency of short movements. The higher frequency of medium to large movements suggests that treeshrews are generally more exploratory in their behavior and are less restricted in their movements than rats. This result is of particular interest, given that there is little comparative information available on movement distances and habitat partitioning in these groups of small mammals (see Emmons 2000, Wells *et al.* 2006a). Rats and treeshrews are known to differ in their life histories. For example, while rats from Borneo use the same burrows or nests for several nights (Wells *et al.* 2006b), treeshrews are known to change their nests nightly (Emmons 2000). Both behaviors suggest that treeshrews are more wide-ranging and visit the same locations less often. However, this idea might not apply to all types of habitats, as treeshrews are also known to frequent favorable sites like fruiting trees and streams (Emmons 2000). Unfortunately, due to the insufficient information available on ranging patterns of rats, we were unable

to test whether larger treeshrew movement distances observed in our study agree with larger ranges recorded elsewhere compared with rats. Nevertheless, extensive tracking data on treeshrews within the same study sites by Emmons (2000), and a tracking study of the rat *Leopoldamys sabanus* as part of our study, shed some light on some aspects of the movement and ranging patterns of these species. Daily distances traveled by treeshrews were estimated as 871 ± 175 m for *T. minor*, 1078 ± 300 m for *T. tana*, 1654 ± 474 m for *T. gracilis*, and 1973 ± 702 m for *T. longipes* by Emmons (2000), while the rat *L. sabanus* was observed traveling a distance of 1443 ± 991 m per night by Wells *et al.* (2008). These values are within the same order of magnitude as the rank of mean movement distances observed in the present study (see Table 1). Whereas the home range estimates reported by Emmons (2000) for the treeshrews in question do not necessarily correlate with movement distances, calculation of minimum and maximum diameter of these home range estimates are again in

the same order of magnitude, although our values are much smaller, with only 11–16% and 20–30% of the home range minimum and maximum diameter estimates, respectively. Consequently, we interpret our data as presenting a meaningful but imprecise insight into a single aspect of movement paths for interspecific comparison, although we stress that conclusions on home ranges based on these data would be premature. Movement distances inferred from live-trapping may include biases, in that trap distance may influence observed movement distances, animals are not free to move around while inside the trap, and they might respond to trapping with trap affinity or avoidance behavior.

Generally, the poor and fragmentary knowledge of most of the examined species precludes an intensive evaluation and interpretation of the available movement data. Yet the various factors that appear to shape the movements of different species add support to the notion that each species has its unique movement pattern, even species pairs similar in size and morphology. Our mixed model approach, which accounted simultaneously for forest type, sex, and age as fixed effects, as well as individual and study site biases, adds support to the notion that movement patterns are driven by various endogenous factors such as sex and age, or exogenous factors such as forest type or site variability.

We suggest that principal relationships between movements and parameters like body size, which have been intensively discussed for mammalian home ranges (McNab 1963, Sutherland *et al.* 2000, Kelt & van Vuren 2001) do not apply to our findings and study species. Rather, we suggest that within the complex rainforest environment, multiple factors may shape movement paths and space-use patterns and cause both inter- and intra-specific variation in space use equivalent to recent suggestions that habitat heterogeneity causes individual movement patterns (see, e.g., Mysterud *et al.* 2001, Jetz *et al.* 2004, Börger *et al.* 2006 for discussion of these aspects).

In summary, we found that small mammal species differ in their movement distances. We suggest that estimates of movement distances from mark-recapture data provide some insight into the movement and ranging of species, although a combination of movement measures with more detailed behavioral observations and life history data are vital for comprehensively understanding space-use patterns. A single estimate of movements provides only a first approximation for environmental practitioners, but

drawing biologically meaningful conclusions faces the challenge of accounting for habitat heterogeneity.

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