

# Analysis of movement and the consequence for metapopulation structure of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Tenebrionidae)<sup>1</sup>

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**Abstract:** The objectives of this study were to examine the movement abilities of the different sexes and the teneral and adult stages of the forked fungus beetle, *Bolitotherus cornutus* Panzer (Coleoptera: Tenebrionidae), to look at whether the beetles move by walking or flying over the scale examined, and to determine the spatial extent of the local or sub-population in a metapopulation context. The capture-mark-recapture method was used within an experimental model system constructed of 90 patches of logs hosting the fungus *Fomes fomentarius* and covering 900 m<sup>2</sup>. Recapture of released beetles did not differ among the groups released, and the analysis revealed that both sexes moved in a similar fashion. Adults moved more often and further than tenerals over the first 28 days of each release. Movement of all individuals was confined to an area roughly 50 m in radius. A percentage of both adults and tenerals had their elytra glued to test for flight in this species. No differences in movement frequency and distance were detected between glued and non-glued individuals. Over 4,000 trap-nights of flight intercept trap data, as well as 15 days over which logs were suspended above the ground, failed to show any evidence of beetle flight. We conclude that *i*) flight is not an important mode of movement over the spatial scale examined, *ii*) adult beetles move further and more often than tenerals, *iii*) most movement is confined to an area of 50 m radius near the release point. Implications for the forked fungus beetle population and metapopulation structure are discussed.

**Keywords:** forked fungus beetle, *Bolitotherus cornutus*, movement, experimental study, metapopulation structure.

**Résumé :** Nous avons examiné les déplacements des adultes et des individus ténéraux mâles et femelles du coléoptère *Bolitotherus cornutus* Panzer (Coleoptera : Tenebrionidae) pour déterminer s'ils se déplacent au sol ou par voie aérienne et pour circonscrire le domaine occupé par une population. Les individus ont été capturés, marqués et recapturés au sein d'un système expérimental constitué de 90 agglomérats de billots abritant le champignon *Fomes fomentarius* répartis sur une superficie de 900 m<sup>2</sup>. Le taux de recapture n'était pas différent selon les groupes, et les deux sexes se déplaçaient de façon similaire. Toutefois, les adultes se déplaçaient davantage et sur de plus longues distances que les individus ténéraux au cours des 28 premiers jours qui suivaient le relâchement des coléoptères après leur capture. De plus, les individus ne se déplaçaient guère au-delà d'un rayon de 50 m. Nous avons collé les élytres de plusieurs adultes et individus ténéraux pour déterminer si cela a un effet sur les déplacements par voie aérienne. Or, nous n'avons détecté aucune différence à cet égard entre les individus aux élytres collés et ceux sans colle. Nous avons aussi tenté d'intercepter au vol les coléoptères grâce à un effort d'échantillonnage de plus de 4000 pièges-nuits et en plaçant des pièges près de billots suspendus pendant 15 jours, mais nos tentatives ont été infructueuses. Nous concluons donc que *i*) le vol ne représente pas un moyen de déplacement important chez *Bolitotherus cornutus*, du moins à l'échelle spatiale étudiée, *ii*) les adultes se déplacent davantage et plus loin que les individus ténéraux et *iii*) ces coléoptères ne se déplacent pas au-delà d'une distance de 50 m de leur point de capture. Nous terminons cet article par une discussion sur les implications de ce travail sur la dynamique des populations et métapopulations de ce coléoptère.

**Mots-clés :** coléoptère, *Bolitotherus cornutus*, déplacement, étude expérimentale, structure d'une métapopulation.

## Introduction

The forked fungus beetle *Bolitotherus cornutus* Panzer in North America and the closely related fungivorous beetle *Bolitophagus reticulatus* L. in Europe are examples of organisms that have proven to be good model systems for investigating various ecological phenomena such as isolation effects (Kehler & Bondrup-Nielsen, 1999), habitat preference (Heatwole & Heatwole, 1968; Sverdrup-Thygeson, 1994; Midtgaard, Rukke & Sverdrup-Thygeson, 1998; Nilsson, 1997), mate choice and sexual selection (Brown & Siegfried, 1983; Brown, Macdonell & Fitzgerald, 1985;

Conner, 1989a), spatial scaling of habitat variables (Rukke & Midtgaard, 1998; Sverdrup-Thygeson & Midtgaard, 1998), and genetic effects of population structure (Whitlock, 1992, 1993, 1994; Knutsen *et al.*, 2000). This system is becoming a powerful method for developing a better understanding of the complicated ecological topics described above. Here we continue this by using the forked fungus beetle to answer the question of population extent by experimentally determining movement abilities.

Care must be taken to define the boundaries of sub-populations that make up a metapopulation. In early metapopulation models, the spatial extent of the sub-populations was not defined, and any discrete group of

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organisms isolated from another discrete group of the same organisms was described as a sub-population in the meta-population sense. For instance, in populations of the forked fungus beetle, which inhabits fungal sporocarps (Liles, 1956), the potential scale of sub-populations may be the log hosting fungal sporocarps or groups of logs with sporocarps separated by increasing distances. Whitlock (1992) suggested that each log constituted a sub-population for the forked fungus beetle. However, he found that with this definition of a sub-population, populations of the forked fungus beetle were genetically in nonequilibrium. He also found that approximately 30% of individuals moved between logs supporting sporocarps and that on average the distance moved was about 17 m. Whitlock's findings suggest that the sub-population extent of the forked fungus beetle potentially covers an area encompassing a group of logs with sporocarps.

Knutsen *et al.* (2000), working with the *Bolitophagus reticulatus*, found that beetle larvae collected from a single log supporting sporocarps were in Hardy-Wienberg equilibrium. This suggests that the population structures of these two Tenebrionid beetles differ, although Nilsson (1997) indicates that an unspecified proportion of adults in a live trapping study moved among birch logs with sporocarps.

A single log supporting fungal sporocarps can be thought of as a habitat patch for both *Bolitotherus cornutus* and *Bolitophagus reticulatus*. Such patches are often scattered within a forest stand such that distances between patches vary from a few metres to several tens of metres. Such a situation seems ideal for a metapopulation context. Past studies have recorded instances of inter-patch movements (defined as moves between logs or a group of logs less than 1 m apart hosting *Fomes fomentarius* [L.: Fr.] Kickx) in forked fungus beetles (Heatwole & Heatwole, 1968; Whitlock, 1992). However, movement between habitat patches has not been explicitly examined. Here, we extend the findings by Whitlock and determine, through experimentation, the extent of a population of the forked fungus beetle given the fragmented nature of the habitat. Specifically, we analyze the movement characteristics of the sexes and test whether newly emerged (teneral) beetles of forked fungus beetles are the dominant movers among habitat patches, an idea first suggested, though not tested, by Whitlock (1992).

To ensure that our experimental design did not miss more vagile individuals and thus underestimate the spatial extent of populations in forked fungus beetles, we performed capture-mark-recapture (CMR) experiments that controlled the ability of individuals to fly and used traps that capture flying insects. We used an innovative method for preventing beetles from flying. Beetles need to open their elytra in order to unfold their wings for flight. We simply glued the elytra shut, thus preventing flight but not otherwise interfering with the beetles' mobility.

CMR studies can be used to quantify movements by following organisms through time and space (Neve *et al.*, 1996; Rudd & McEvoy, 1996; Turchin, 1998). By recapturing an organism and recording its new spatial and temporal co-ordinates, a collection of moves, or path, can be constructed. By analyzing this path, a great deal of information can be interpreted about how an organism moves in its envi-

ronment. Correlated Random Walk (CRW) provides a powerful method for analyzing path data (Kareiva & Shigesada, 1983). Deviations from the expected CRW response can be interpreted to investigate how both individuals and populations of organisms are moving in their environment.

Here, we 1) determine the frequency and distance of inter-patch movement; 2) test whether tenerals move more often and further than adults, by marking and following the movements of the forked fungus beetle; 3) investigate whether individuals move by flight or by walking at the scale of up to 100 m through experimental manipulation of flight ability; 4) compare male and female movement dynamics; and 5) combine analysis of the above factors to determine spatial spread of a population by comparing actual and theoretical movements. We then discuss the implications of considering the spatial scale of a population for metapopulation dynamics in the forked fungus beetle.

#### STUDY ORGANISMS

The forked fungus beetle lives on the sporocarps of the bracket fungi *Fomes fomentarius*, *Ganoderma applanatum* (Persoon) Patouillard, and *Ganoderma tsugae* Murrill (Pace, 1967; Mathewman & Pielou, 1971). During the summer breeding season, females lay approximately 20 eggs on the surfaces of these fungi, and the larvae tunnel through the sporocarp to feed. Adults feed on the underside (Liles, 1956) of the fungi. Both adults and young survive the winter within the sporocarps (Liles, 1956; Pace, 1967). Only males have pronotal horns, which may vary in size, making it easy to sex individuals in the field (Liles, 1956; Heatwole and Heatwole, 1968). Flight in this species has only been recorded once, and then under very artificial conditions (Teichert, 1999). Individuals measure about 10 mm in length and for the purposes of this study, were harmlessly and permanently marked with enamel paint. Sporocarps last for up to 10 years (Schwarze, 1994) and are thus a potential resource for several generations of beetles.

#### Methods

An experimental model system (Ims & Stenseth, 1989; Wiens *et al.*, 1993) was constructed, consisting of a spatial arrangement of *F. fomentarius* fungal sporocarps in a forested environment.

Logs hosting sporocarps of *F. fomentarius* were collected from locations in western Nova Scotia, Canada by cutting host trees with a chainsaw to allow for continued growth of the fungus after removal from its *in situ* location. Logs were chosen by looking for live sporocarps in intact condition. Sporocarps in this state were most often used by forked fungus beetles as mating arenas, food sources, and oviposition sites (Bondrup-Nielsen, pers. obs.). Each log measured 40 to 70 cm in length and 10 to 40 cm in diameter.

The study site consisted of 90 logs arranged in a 9 by 10 grid with 10-m spacing. Each log could then be identified by a unique row and column code. This scale was chosen to cover an area that would encompass much of the movement by *B. cornutus*, based on extensive earlier observations of the maximum movements of this species in similar settings

in Nova Scotia (Bondrup-Nielsen, unpubl. data). No barriers were placed on the perimeter, and organisms could move on and off the site. This experimental model system was located in a well-drained, mixed wood forest on the South Mountain, King's County, Nova Scotia (45° 5' N, 64° 25' W).

Adult beetles used in the experiment were collected from locations in western Nova Scotia by visiting sites where large populations of *F. fomentarius* and *G. applanatum* were found. Beetles were found on the fungal sporocarps and taken back to the lab to be marked. Teneral were collected as larvae with their associated sporocarp in the autumn and winter of 1998/early 1999 from several different sites in western Nova Scotia and raised over the winter. Sporocarps were chosen by looking for ones with large numbers, typically from 5 to 20, of the characteristic eggs of the forked fungus beetle on the cuticle. The sporocarps were stored in a caged, outdoor room at Acadia University's animal care facility. Teneral began to emerge from the sporocarps in late July 1999 and were then collected and marked for release.

To distinguish individuals, all beetles were marked using Testor's Non-Metallic Enamel Paints prior to release in the study area. Each was given a unique pattern of five coloured dots, one on the pronotum and two on each elytra.

To test whether teneral move more often and further than adults, both adult and teneral forked fungus beetles of both sexes were released into the experimental model system.

Six releases of beetles were conducted, all on the study site logs hosting *F. fomentarius* (Table I). In each of the releases, half of the beetles were male, and half were female. Four solely adult releases were conducted, followed by 2 teneral releases, each of which consisted of 30 teneral and 30 adults. A thorough search for beetles at all potential habitat sites (sporocarps) in the study area was made daily from 10 June to 15 September. At each sighting (recapture) we recorded the colour code of the beetle and its location on the grid. All searches were conducted in the early morning and lasted for 70 to 80 minutes. Introduced beetles from previous releases were not removed from the experimental model system when new releases were conducted.

To determine if flight was occurring, we prevented some of the released beetles from flying, suspended logs with sporocarps in the air, and attempted to capture flying beetles in flight intercept traps.

Prevention of flight was accomplished by using Elmer's 5-minute Epoxy glue to seal the suture between the elytra on the dorsal side of selected individual beetles. A small dab of glue over the elytral suture (less than 1 mm by

1 mm) was used. In field trials, this proved an effective method, with only 2 individuals (~3%) showing signs of glue spots deteriorating to the point where the individual might be able to open its elytra. However, no beetle, glued or otherwise, was ever observed in flight.

Forty-five flight intercept traps were used to capture flying beetles. These traps consisted of interlocking, perpendicular panels of transparent Plexiglas measuring 60 cm tall by 30 cm wide, with a conical collecting base that ended in a plastic container. The plastic collecting container consisted of an unbaited 100-ml plastic jar filled with 10% ethylene glycol to preserve captured invertebrates. These traps were suspended as near as possible to the experimental *F. fomentarius* patches on the release grid, at 3 heights: canopy (within 1 m of the tops of trees, at approximately 10 m above the forest floor), mid-canopy (on average, 5 m above the forest floor), and 50 cm above ground. A staggered pattern was used, with the traps placed above every second patch location. Fifteen of each class of traps were used, in a repeating pattern of ground, mid-canopy, and canopy heights. A total of 4365 trap days were recorded among the three classes of traps. The traps were sampled, and invertebrates greater than 0.25 mm, large enough to be distinguished as invertebrates using a Wild™ dissecting microscope at 25X, were recorded.

As another method of testing for flying beetles, beginning 1 September and continuing to 15 September, half of the logs were suspended 1 m above the ground using heavy-gauge twine tied to tree branches. Any forked fungus beetles that were resident on these patches were removed and released on the ground directly below the suspended logs, and could only return to the logs by flight. Each hung patch was visited daily during the normal course of checking the experimental site.

The analyses of the forked fungus beetle movement data were conducted using non-parametric Kruskal-Wallis tests (Zar, 1996), followed by Nemenyi multiple comparisons (Zar, 1996), Z-tests, and Autocorrelation Function (ACF) in S-Plus Professional 4.5 (Mathsoft, 1998). Further model fitting was done using the Correlated Random Walk framework, after Kareiva and Shigesada (1983) and Turchin (1998). Each class of beetle (for instance, Adult with Glued Elytra, Adult with Non-glued Elytra, Teneral with Glued Elytra) was tested against each other class using the Kruskal-Wallis tests, with Nemenyi multiple comparisons used to locate the significant differences.

## Results

Analyses were based only on data from the first 28 days of each release to standardize the number of days of moves between each treatment. This was done because the last release of teneral only covered 28 days. Analysis of net squared displacement (NSD) data plotted against time indicated that movement for forked fungus beetle individuals tended to level off near 28 days, with the majority of moves taking place in the first 30 days after release (Figure 1). In a random walk framework, this curve is expected to increase linearly with time (Turchin, 1998). A levelling-off of NSD with time is consistent with an organism settling down in a

TABLE I. Summary of experimental treatments (Sex – Male, Female; Age – Adult, Teneral; Glue – Glued elytra, Non-glued elytra) for the different releases.

Release	Date	Treatment	Sample size
Adult 1	10 June	Sex	60
Adult 2	17 June	Sex	60
Adult 3	27 June	Sex, Glue	60
Adults 4	11 July	Sex, Glue	60
Teneral 1	3 August	Age, Sex, Glue	60
Teneral 2	20 August	Age, Sex, Glue	60

territory or reaching the limits of its movement ability (Turchin, 1998). Because the vast majority of moves (98%) we measured were much less than 50 m, we are confident that the levelling off of the NSD that we found is actually part of the system, not an artefact of the experimental set-up.

A high proportion (minimum 82%) of individuals in all releases were resighted (Table II). To compare the between-release observations, a resightability measure was calculated to judge the equality of resighting between releases. Resightability (R) was calculated using the following equation:

$$R = (N - 1)/(T) \quad [1]$$

where N is the number of days resighted, and T is the total days it could have been resighted. No significant difference in resightability among the 6 groups was detected (Table II,  $F = 0.50$ ,  $df = 5$ ,  $p = 0.78$ ).

When the step lengths (distance moved between resightings) of adults were considered, 341 of 347 step lengths (98.3%) were less than 50 m in length, and only 5 of 184 individuals (2.7%) made moves greater than 50 m. All teneral moves were less than 50 m. Time between resightings varied from 1 to 65 days.

A Kruskal-Wallis test conducted on the mean move distances of each individual in unglued treatments of teneral and adult forked fungus beetle (Figure 2) showed there was a significant difference between male and female teneral and adult beetles ( $\chi^2 = 14.7$ ,  $df = 3$ ,  $p = 0.02$ ). The non-parametric Nemenyi multiple comparisons test was used to locate the individual differences between groups, with significant differences in move distance shown between Female Adult and Female Teneral ( $p < 0.005$ ) and between Male Adult and Male Teneral ( $p < 0.02$ ).

Among tenerals and adults, there was no significant difference in mean distance moved by either glued or non-glued males and females ( $\chi^2 = 1.64$ ,  $df = 3$ ,  $p = 0.65$ ,  $\chi^2 = 2.05$ ,  $df = 3$ ,  $p = 0.56$ , respectively). There thus appears to be no difference in move distance between the different sexes in the forked fungus beetle at the 100-m scale measured in this study. Also, the glued and non-glued beetles

showed no difference in move distance, suggesting that the movement at the scale measured is by walking, not flight.

Over 5,800 macro-invertebrates (defined as invertebrates larger than 0.25 mm) were captured in flight intercept traps suspended above the ground during the experiment, which covered 97 nights. More than 2,000 of these were Coleoptera. No forked fungus beetles were recorded.

For the last 15 days of the experiment, half of the target logs in the experimental model system were suspended 1 m above the forest floor, and the forked fungus beetle individuals inhabiting them were removed and placed on the forest floor below the log. No forked fungus beetles were recorded

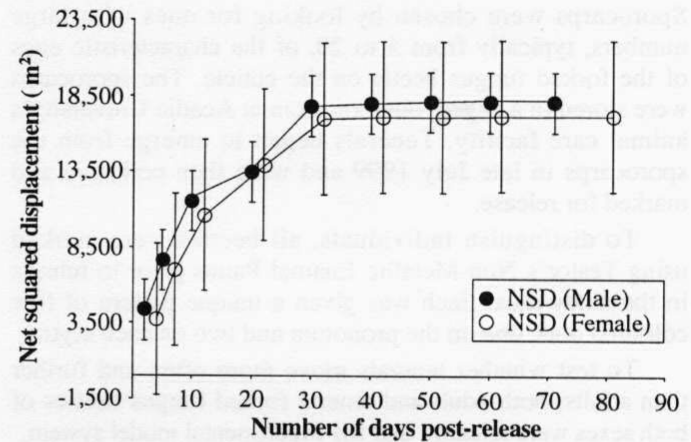


FIGURE 1. Net squared displacement (NSD) of all glued individuals. Note that an asymptote is reached at 30 days post-release. Bars around theoretical NSD points are 95% confidence intervals.

TABLE II. Parameters for experimental treatments.

Release	Proportion moving*	Resightability $\pm$ SD*	Mean Distance (m) $\pm$ SD*	Proportion resighted*
Adult 1	0.86	0.34 $\pm$ 0.21	15.18 $\pm$ 13.85	0.85
Adult 2	0.88	0.34 $\pm$ 0.25	11.65 $\pm$ 9.93	0.82
Adult 3	0.95	0.40 $\pm$ 0.26	12.74 $\pm$ 12.28	0.98
Adult 4	0.86	0.42 $\pm$ 0.28	12.32 $\pm$ 10.41	0.98
Teneral 1	0.49	0.37 $\pm$ 0.28	5.43 $\pm$ 2.56	0.95
Teneral 2	0.44	0.43 $\pm$ 0.29	5.36 $\pm$ 6.08	0.95

\* calculated using first 28 days of release

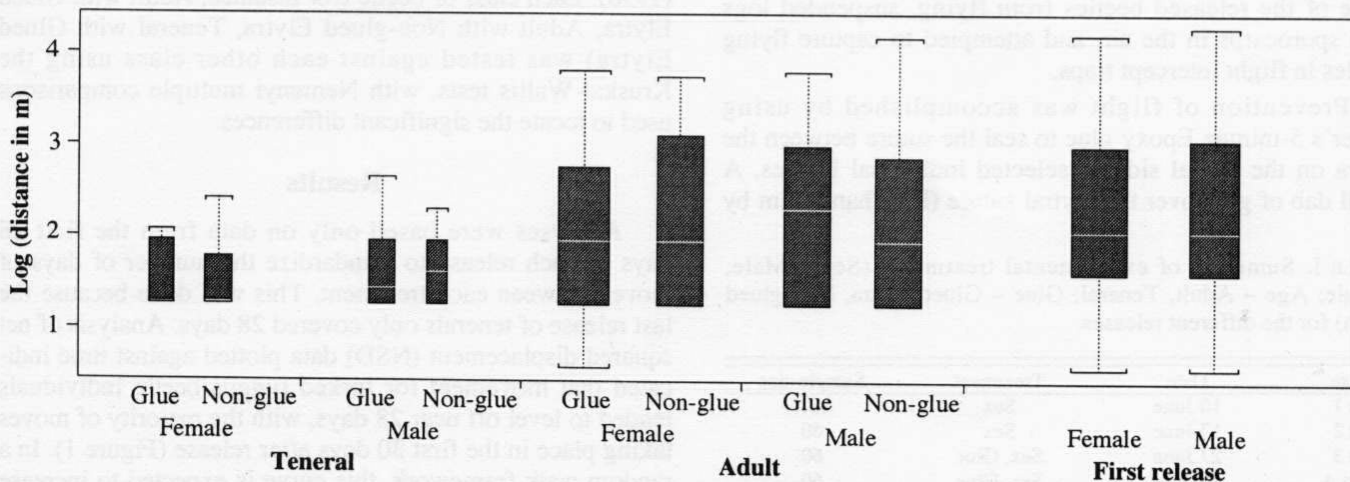


FIGURE 2. Log-transformed movement data for first 28 days of each treatment release. White line is the median, box encloses 1 SD on either side of the mean, outer bars enclose 95% of the data, width of bars is proportional to number of moves represented for each class of beetles.

recolonizing these logs, though 16 (35.6%) had been occupied by a total of 71 beetles prior to the hanging of the logs.

Because no difference was found between the sex and glue classes, correlated random walk analysis, outlined in Kareiva and Shigesada (1983) and Turchin (1998), was conducted using the pooled data from all releases in both adult and teneral classes. Theoretical Net Squared Displacement (NSD,  $\hat{y}_n^2$ ), calculated using equation 2, was plotted against the number of moves and compared with the observed NSD. Observed NSD was calculated by averaging  $\hat{y}_n^2$  for each different  $n$  (move number) (Kareiva & Shigesada, 1983). Theoretical NSD was calculated as follows:

$$\hat{R}_n^2 = nm_2 + 2m_1(\psi/1 - \psi) \times (n - (1 - \psi^n)/(1 - \psi)) \quad [2]$$

where  $m_1$  is the mean move length,  $m_2$  the mean squared move length,  $\psi$  the average cosine of the turning angle, and  $n$  the number of moves. The data used to construct the theoretical NSD came from the movements found on our experimental grid; thus, the theoretical NSD will predict the maximum NSD allowed in a similar-sized region.

Confidence intervals for the theoretical NSD were computed by bootstrapping 1,000 samples of the calculated NSD for all moves at each  $n$  to produce a standard error for each  $n$ . This standard error was then multiplied by the appropriate two-tailed  $t$ -value to produce a confidence interval for the theoretical NSD at each move number (Efron & Tibshirani, 1993; Davison & Hinkley, 1997; Turchin, 1998; Venables & Ripley, 1999). A Z-test was performed on each pair of values (one each from the observed and theoretical NSD) to test for differences between theoretical and observed NSD. For adults, higher order autocorrelations in the turning angles (*i.e.*, autocorrelations in turn angle above lag 1) were calculated. Following the methods in Turchin (1998), these autocorrelations were computed using formula 3:

$$\text{Autocorrelation measure} : (S - O)/(S + O) \quad [3]$$

where  $S$  is a pair of turns in the same direction, and  $O$  is a pair of turns in the opposite direction. All possible pairs of turning angles were calculated for each lag (2 through 6 here) and assigned to one of two categories:  $S$ , turns in the same direction (left-left, right-right, or no turn);  $O$ , turns in opposite direction (left-right or right-left). For each lag  $d$ , a value between -1 and 1 is calculated, with -1 indicating full negative autocorrelation between turn angles at lag  $d$  and 1 indicating full positive autocorrelation between turn angles.

Figures 3 and 4 show the results of plotting Net Squared Displacement against number of moves for adults and tenerals. Both adult and teneral theoretical NSDs over-predicted the spatial spread of the population (Z-test for adults, all  $p$ -values < 0.001). The autocorrelation measure for turn direction was calculated for the adult, but not teneral, forked fungus beetle due to the larger number of moves in the adult age class. Autocorrelation in turn direction for adult forked fungus beetle reached maximums at lags 5 and 6, where there was maximum positive autocorrelation in turn direction (that is, turns separated by lags of 5 and 6 were most likely to be in the same direction) (Table III).

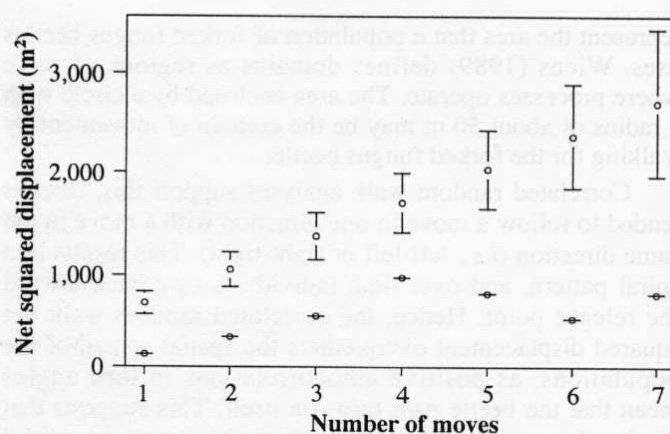


FIGURE 3. Theoretical net squared displacement ( $m^2$ ) (open circles) and actual net squared displacement ( $m^2$ ) (circles with horizontal bars) versus number of moves, for all adult *Bolitotherus cornutus*. Bars around theoretical NSD points are 95% confidence intervals.

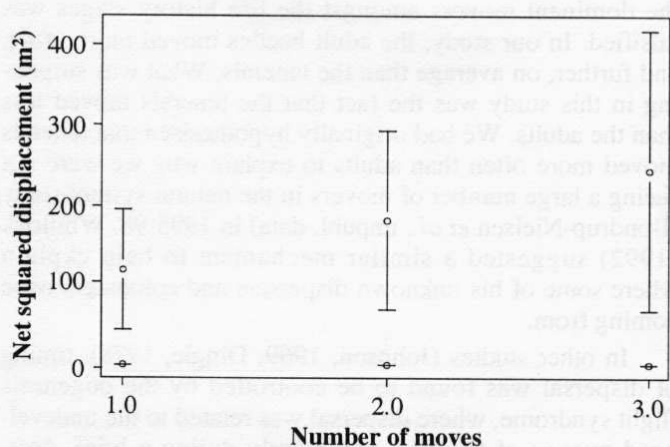


FIGURE 4. Theoretical net squared displacement ( $m^2$ ) (open circles) and actual net squared displacement ( $m^2$ ) (circles with horizontal bars) versus number of moves, for all teneral *Bolitotherus cornutus*. Bars around theoretical NSD points are 95% confidence intervals.

TABLE III. Autocorrelation measure for each lag  $d$  for adult forked fungus beetles.

Lag ( $d$ )	2	3	4	5	6
Mean	-0.014	0.321	0.111	0.810	0.857
SE	0.736	0.736	0.469	0.091	0.051
$n$	61	28	9	7	7

## Discussion

This paper provides unequivocal evidence that the subpopulation extent of the forked fungus beetle encompassed groups of logs with sporocarps. A high proportion of individuals released, especially adults, moved between patches. Whitlock (1992) also found a high proportion of movers, though most of his results are from a short-lived study where sporocarps were nailed to trees. These sporocarps became mouldy after less than two weeks (Whitlock, 1992). Our experiment expands on his results by presenting data from live sporocarps over a much longer time period (91 days). Also, the experimental set-up of this study consisted of birch log sections with intact sporocarps; the sporocarps did not go mouldy but stayed alive. An area with a radius of approximately 50 m contained the majority of forked fungus beetle movements in this study. This may

represent the area that a population of forked fungus beetles uses. Wiens (1989) defines domains as regions of scale where processes operate. The area enclosed by a circle with a radius of about 50 m may be the domain of movement by walking for the forked fungus beetle.

Correlated random walk analyses support this. Beetles tended to follow a move in one direction with a move in the same direction (*i.e.*, left-left or right-right). This results in a spiral pattern, and over time individuals turn back toward the release point. Hence, the correlated random walk net squared displacement overpredicts the spatial spread of the populations, as positive autocorrelations in turn angles mean that the beetle path turns on itself. This suggests that the beetles confine their movements to a certain spatial extent, as the number of direction reversals increases with move number.

Our conjecture that teneral forked fungus beetles were the dominant movers amongst the life history stages was falsified. In our study, the adult beetles moved more often, and further, on average than the teneral. What was surprising in this study was the fact that the teneral moved less than the adults. We had originally hypothesised that teneral moved more often than adults to explain why we were not seeing a large number of movers in the natural system study (Bondrup-Nielsen *et al.*, unpubl. data) in 1995-98. Whitlock (1992) suggested a similar mechanism to help explain where some of his unknown dispersers and colonizers were coming from.

In other studies (Johnson, 1969; Dingle, 1978), timing of dispersal was found to be controlled by the oogenesis flight syndrome, where dispersal was related to the undeveloped ovaries of females, particularly during a brief, post-teneral period (Messina, 1982). However, the life history of the forked fungus beetle differs markedly from the insects in the above studies. For example, the goldenrod leaf beetles *Trirhabda virgata* LeConte and *T. borealis* Blake (Coleoptera: Chrysomelidae) studied by Messina (1982) had a maximum life span of about 7 months. The forked fungus beetle can live up to 5 years and overwinters in diapause several times (Bondrup-Nielsen, pers. obs). Teneral forked fungus beetles may need to overwinter once to reach sexual and physical maturity, at which time they have the fully developed musculature necessary for movement.

The experiment where the elytra were glued suggests that most or all of the movement observed among the sporocarp-covered logs in the experimental model system was by walking. This is further supported by the complete lack of captures of forked fungus beetles in flight intercept traps and also the absence of individuals colonising (or returning to) logs suspended above the forest floor.

The area enclosed within a circle of 50 m radius suggests the scale at which a population of the forked fungus beetle should be defined. Previous studies (Heatwole & Heatwole, 1968; Conner, 1989b; Whitlock, 1992, 1994) have considered the forked fungus beetle populations to be confined to one fungus-hosting log or a group of fungus-hosting logs separated by less than 1 m. This study suggests that the population definition should be expanded to include all the forked fungus beetles inhabiting *F. fomentarius* patches within an area with a 50 m radius. Also, the move-

ment between patches within this scale is not dispersal, but simply movement within a home range. The metapopulation concept applied to the forked fungus beetle in the wild should be modified. This study demonstrates that a sub-population of the forked fungus beetle potentially encompasses a number of separate patches of birch logs infested with the tinder fungus. This suggests a new heuristic for considering forked fungus beetle population scale and spatial structure. It also points to the need to carefully consider the spatial scale of the sub-population in describing a system as a metapopulation.

Studies of the forked fungus beetle illustrate this last point. When the original definition of sub-population in this species is used (Heatwole & Heatwole, 1968; Whitlock, 1992), the sub-populations exist as all beetles found on one log or on a group of sporocarp-bearing logs separated by less than one metre. In contrast, the results of this study suggest that all beetles found in an area within a radius of at least 50 m should be considered a sub-population in the metapopulation sense. This drastically changes the metapopulation structure of, say, a 1-hectare forest that contains forked fungus beetles. Now the entire forest can be thought of as containing one metapopulation, consisting of several distinct sub-populations encompassing areas within the forest. Examining population dynamics at the proper scale is thus critically important. For instance, if we underestimate movement, too much focus may be placed on small-scale habitat units (in the present case, on one log or group of logs spaced less than 1 m apart) when in fact the life-history of the organism depends on large-scale habitat for persistence. If dispersal is overestimated, we may overestimate an organism's ability to move to distant habitats. In species management terms, either of these predictions may ultimately be disastrous: too much emphasis may be placed on the small-scale habitat in the former case, and in the latter, it may be assumed that a species can recolonize/colonize vacant habitat when in fact it is beyond the organism's reach.

Further, scale is important to metapopulation persistence over time. If the area in which the metapopulation exists becomes too small, through a disturbance or other mechanism, the persistence of the entire system may be in jeopardy. Sub-populations in the metapopulation sense are recognized to disappear or go extinct through time, for a variety of reasons (Hanski & Gilpin, 1997). If there are no nearby sources of colonists to maintain a sub-population or repopulate it (rescue effect: Brown & Kodric-Brown, 1977), the sub-population may not be maintained or re-established. Thus, when considering organism distributions across a landscape, persistence might be better ensured by low to medium densities resulting from a number of smaller sub-populations across a large region than by high-density local populations. The importance of autecological data for individual organisms remains very important in examining problems of this type.

A comparative study of *Bolitophagus reticulatus* should be carried out. Nilsson (1997) found in his live capture study that some adults moved among patches. Why then did the study by Knutsen *et al.* (2000) find that populations at the spatial scale of a single log with sporocarps were in Hardy-Wienberg equilibrium? Understanding the move-

ment dynamics of *Bolitophagus reticulatus*, which fundamentally occupies the same niche as the forked fungus beetle, could lead to a fuller understanding of the factors that influence movement.

The forked fungus beetle appears to move by walking over distances up to 50 m. However, it does colonize forest fragments isolated by several hundreds of metres. It may be that this species exhibits two scale-dependent modes of movement, as first proposed by Kehler and Bondrup-Nielsen (1999). Above the 50 m distance, movement may be dominated by flight, instead of walking. While this study found no evidence of individuals flying, flight has been recorded in the past (Teichert, 1999). Though capture-mark-recapture experiments tend to oversample less-vagile individuals (Turchin, Odendaal & Rausher, 1991), we attempted to reduce this sampling error by using flight intercept traps and hung logs to look for flying forked fungus beetles. After much sampling effort, no flying forked fungus beetles were found. Perhaps flight in the forked fungus beetle is used only in longer-distance dispersal events, especially in highly fragmented landscapes, where individuals are forced to cross an inhospitable matrix.

An alternative explanation for the lack of flight observations may be related to the experimental model system. Because individuals could only be sampled at introduced patches of *F. fomentarius*, beetles making movements that did not involve stopping on these patches would be under-sampled. Such would be the case if female forked fungus beetles were moving according to the oogenesis-flight syndrome (Johnson, 1969; Dingle, 1978), where individuals do not typically respond to food or oviposition sites (in this case, the *F. fomentarius* sporocarps). Some individuals may well have left the grid, and their movements could constitute dispersal. However, with no data on this, no conclusions can be drawn. The area surrounding the grid up to 50 m was searched extensively, and we did not find any patches of *F. fomentarius* sporocarps that the beetle could have occupied.

In conclusion, we found that movements of beetles seem to be confined to an area with a radius of approximately 50 m; this may represent a better spatial definition of forked fungus beetle sub-population structure. There was no evidence that tenerals are the dominant dispersers in forked fungus beetle populations; in fact, the data suggest that the adult beetles move more often and further. There is no distinct difference in movement between the sexes, as both males and females move at a similar rate. Flight does not seem to be an important mode of movement, at least at the scale considered in this experiment. Finally, there was no difference in movement rate or distance between beetles with glued and non-glued elytra.

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