LARVAL HABITAT AND REINTRODUCTION SITE SELECTION FOR *CICINDELA PURITANA* IN CONNECTICUT

KRISTIAN SHAWN OMLAND [1,2]

ABSTRACT - For *Cicindela puritana* to be a viable member of New England's biota, there must be more than the current two occurrences. Assessment of the chance that the species can spread, whether on its own or through reintroduction, required identifying vacant habitat patches, which in turn, required refining the description of the species' larval habitat. Analysis of larval microhabitat variables identified sand texture as the most important determinant of habitat suitability. I then surveyed a 79 km stretch of the Connecticut River in Connecticut looking for suitable habitat patches. Of 32 beaches, none that appeared to be suitable was nearer than 12 km from currently occupied patches. Dispersal is unlikely to lead to establishment of new populations, so I recommend reintroducing *C. puritana* to an area in the vicinity of Windsor, CT where there are beaches on three islands that appear to be suitable larval habitat.

INTRODUCTION

The number of Puritan tiger beetle (*Cicindela puritana* G. Horn) populations has declined precipitously in the last century. One hundred years ago, there were no fewer than twelve populations (or metapopulations) on the Connecticut River (as represented by specimens in collections); by the late 1980s there were precisely two and the species was listed as threatened under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1993).

Assessment of the viability of the species on the Connecticut River needs to be done on two levels: local populations and regional occurrence. Abundance in the two extant populations has been monitored since concern about the species' status arose in the late 1980s. The metapopulation in Cromwell-Portland, Connecticut has remained remarkably stable at 400–700 individuals (maximum counts of adults, an index of relative abundance; pers. comm., P. Nothnagle, Windsor, VT). Formal population viability analysis has indicated that that population is unlikely to decline significantly in the next 30 years (Omland 2001). The population in Northampton, MA has also remained remarkably stable, but at precariously low numbers (fewer than 20 adults enumerated by marking all individuals; pers. comm.,

[1] University of Connecticut, Department of Ecology and Evolutionary Biology, Storrs, CT 06269. [2] current address - School of Natural Resources, University of Vermont, Bulrington, VT 05405; kristianomlnd@uvm.edu.

C. Davis, Shutesbury, MA); abundance there would have to increase by an order of magnitude before it could be viewed as safe from imminent extinction.

When assessing regional viability, one must consider both the annual probability that each population (or metapopulation) will go extinct and the annual probability that a new population will be founded. If local extinctions occur independently and there is a negligible probability that a new population will be founded, the probability of regional extinction can be estimated as the product of the probabilities of local extinctions; under those assumptions, adding a population significantly diminishes regional extinction risk. Given that potential disturbances on a river would be correlated (e.g., floods, pollution events), however, the probabilities of local extinction may not be independent. Nonetheless, the general principle of spreading the risk holds: risk of regional extinction is lower if there are more populations (den Boer 1968). As put forward in the recovery plan for the species (U.S. Fish and Wildlife Service 1993), establishing additional populations of Puritan tiger beetles on the Connecticut River is a central recovery goal.

New populations can be founded by individuals that emigrate from an extant population and fly to the new site, or they can be established through a reintroduction program (Kozol et al. 1996; Nicholls and Pullin 2000; Wynhoff 1998). In order to assess the probability of success via either route, we need to know whether and where suitable vacant habitat patches exist along the Connecticut River. If there are vacant patches close enough to existing populations, natural colonization may occur, but, if there are not, we need to know the locations of candidate beaches for reintroduction. Therefore, one of my purposes in this study was to survey potential colonization and reintroduction sites.

Before we can identify suitable habitat patches, we must know what makes a patch suitable. In a broad sense, habitat for Puritan tiger beetles is sandy beaches on large bodies of fresh or brackish water, i.e., along the Connecticut River and Chesapeake Bay (Knisley and Schultz 1997, Leonard and Bell 1999, U.S. Fish and Wildlife Service 1993, Wickham 1899). However, a more refined understanding of the species' habitat requirements is needed. That task can be accomplished by measuring one or more indicators of fitness (e.g., survival, recruitment) or surrogates thereof (e.g., density, incidence) in a variety of locations representing a range of potentially relevant environmental variables, and then determining the combination of environmental variables where fitness is high. Incidence and density are easiest to measure, but determining habitat suitability from them requires caution because of source-sink dynamics (Pulliam 1988, Thomas et al. 1996) and other reasons. Despite such problems, describing patches that currently have high density is a good place to start in the context of an adaptive management program

(Haney and Power 1996). Information about the success or failure of colonization opportunities, reintroduction efforts, or both should then be used to refine the description of suitable habitat.

Tiger beetles, like most holometabolous insects, spend the majority of their life cycle in the larval stage. Larval tiger beetles are essentially sessile, passing their entire two-year development where their mother places the egg, or at least near that point. Adults, on the other hand, are decidedly vagile, being well-known as fast runners and strong flyers (Knisley and Schultz 1997; Leonard and Bell 1999). Adult Puritan tiger beetles have been observed foraging, mating, and burrowing in the same areas where larvae are found. In addition, the more vagile adults are often encountered in areas adjacent to those occupied by larvae, but such areas are probably unsuitable for larvae, especially outside of the flight season (i.e., winter). In general, it is thought that tiger beetle larvae have narrower tolerances for physical environmental factors than adults do (Pearson 1988). Therefore, my other purpose, which is a prerequisite for surveying potential habitat patches, was to establish a quantitative description of suitable larval habitat for Puritan tiger beetles.

METHODS

Larval habitat description

I identified beaches by river km and bank. River km measured from the mouth of the river was interpolated from values for prominent landmarks given in Borton (1990). Bank was identified from the perspective of an individual traveling downstream, that is, the left bank was generally to the east and the right bank to the west; beaches on islands were simply designated with the letter I. Thus, each beach was identified by a code such as 50-R (river km 50 on the right bank) or 91-I (river km 91 on an island). Distinct subsections of beaches were given lowercase letter modifiers, e.g., 50-R(a).

Puritan tiger beetle larvae excavate burrows in sand that are distinguishable from burrows of other species of tiger beetles and other arthropods based on characteristics of the mouth of the burrow as well as its orientation and depth. I counted larvae non-intrusively by probing holes in the sand with a stem of grass to determine whether they matched the characteristics of Puritan tiger beetle larval burrows. The criteria that I used were 1) a nearly round, neatly maintained hole, 2) vertical orientation, and 3) generally at least 20 cm deep. The first criterion distinguished tiger beetle larval burrows from those of other arthropods (Knisley and Schultz 1997). The latter two criteria were unambiguously associated, in almost all cases, with vertical, deep burrows belonging to *C. puritana* and angled, shallow burrows belonging to either *C. repanda* or *C. hirticollis* (pers. comm., P. Nothnagle, Windsor, VT).

A low intensity study entailed counting larval burrows in quadrats at four beaches in the river km 46–50 metapopulation (50-R[b, c], 49-I, 47-R, and 46-L). Since tiger beetle larvae generally occupy the same burrow throughout their larval growth, I assumed that there was a 1:1 correspondence between the number of burrows and the number of active larvae. I considered larvae to be active if the mouths of the burrows were open (larvae sometimes plug the mouth of their burrows). I made one set of counts in 1 m X 1 m quadrats on 7–8 October 1999, and two other sets of counts in 0.5 m X 0.5 m quadrats on 6 September and 20 September 2000. In general I located the quadrats on a regular grid at each beach, although at 47-R I resorted to selectively placing quadrats in areas where I saw some larvae or where the microhabitat appeared suitable. I compared density using the non-parametric Kruskal-Wallis test, and computed the correlation between density and sand texture (described below).

I did a multiple regression analysis of density as a function of a number of candidate explanatory environmental variables based on data from a more intensive study at two of the beaches (50-R[b] and 46-L). I counted larval burrows in 2 m wide belt transects laid across the beaches perpendicular to the river, which I surveyed biweekly from 1 June through 15 October, 1999. The activity level of Puritan tiger beetle larvae was almost nil during midsummer, but there was a dramatic increase in the number of active larvae between the weeks of 23 August and 13 September (unpub. data, reconfirmed with less quantitative observations in 2000; also pers. comm., P. Nothnagle, Windsor, VT); therefore I viewed measurements of larval density from surveys during September and October as the best indicators of larval density in each of the transects. Individuals represented by an open burrow on any of three survey dates were counted. I avoided counting individuals multiple times by using numbered tags, and by associating individuals of the same instar that appeared within 5cm of the location of a previously recorded individual whose tag had been displaced.

I collected 200–300 g samples of sand from the surface and at a depth of 30 cm from a regular grid spread across each of the beaches. The points were not within transects, but were close to them (0.5 or 5 m in most cases, 15 m in one case). I put the sand into a labeled paper bag, which was rolled up and sealed in an individual plastic bag. The packets were transported to the laboratory in an insulated box, and weighed within 24 hours. I then weighed the sand in the paper bag, placed it in a drying oven at 70 °C for 48–72 h, and weighed it again subtracting the weight of the dry paper bag. I also weighed the plastic bag at the time I removed the fresh sample and after the sample had been dried to account for moisture that collected in the plastic bag as condensation. The weight lost was an estimate of the mass of water in the original sample, which I expressed as the proportion of the total mass of the original sample.

Dried sand samples were spooned into a stack of hand-held sieves that separated particles larger than 1 mm, 0.5 mm, 0.25 mm, and 0.125 mm; a cup at the base of the stack collected finer particles. The five fractions were labeled "very coarse," "coarse," "medium," "fine," and "very fine" (McCullough 1984). I shook each sample by hand for 5min, and weighed each fraction. I conducted a principal components analysis (PCA) on the samples to condense the five-fraction measurement to a lower-dimensional measure of sand texture.

I measured cover at two to four evenly spaced points along each transect that were clearly within the beach (i.e., not below the high tide line or above the crest of the bank). I used a 0.5 m X 0.5 m quadrat with two sets of five crosshairs that identified 25 evenly distributed points within the quadrat. By sighting directly down the intersection of the two sets of crosshairs, I unambiguously identified a precise point on the ground that I classified as sand, plant (initially in finer categories), or detritus. I entered the fraction in each of the three classes into the analysis.

Finally, I measured potential prey availability by drawing a 1-m radius circle in the sand at evenly spaced points along each transect, which I stared at for 3 min counting the number of potential prey items while avoiding counting the same individual multiple times. I categorized the animals by size (small = head diameter less than about 1 mm; medium = head diameter between about 1 and 2 mm; large = head diameter greater than 2 mm) and made notes about their identity (usually family level).

I performed a multiple regression analysis in S-Plus using a stepwise selection procedure. Terms were added if Akaike's information criterion (AIC) was lower for the fuller model. Separate analyses were done for two sets of candidate models with respect to sand texture. The first set had the fraction of particles in each size class as potential explanatory variables, the second had the significant principal components of sand texture.

Reintroduction site selection

I canoed the Connecticut River from Springfield, MA (river km 113) to East Haddam, CT (river km 24) searching for sandy beaches. I stopped at each beach that was at least 2 m wide and 30 m long; I also recorded data about a few smaller beaches. On days when the water was low, I considered only the area above the recent high water mark, as represented by a line of debris. The water was unusually high on several of the days when I was on the river; on such days, I stopped at beaches that appeared smaller and attempted to account for areas of normally exposed sand.

At each beach, I used a GPS receiver to obtain an exact (± 20 m) fix on its location. I visually estimated the size of the area of open sand and described its shape and topography. I described the sand and took samples back to the lab as above. Fractions in each particle size class were averaged among the samples from a beach and normalized so that they added up to one. Plant growth and detritus were described, and adjacent land cover was noted (i.e., forest, grassland, agricultural land, industrial land). Recreational use of each beach was evaluated by look-

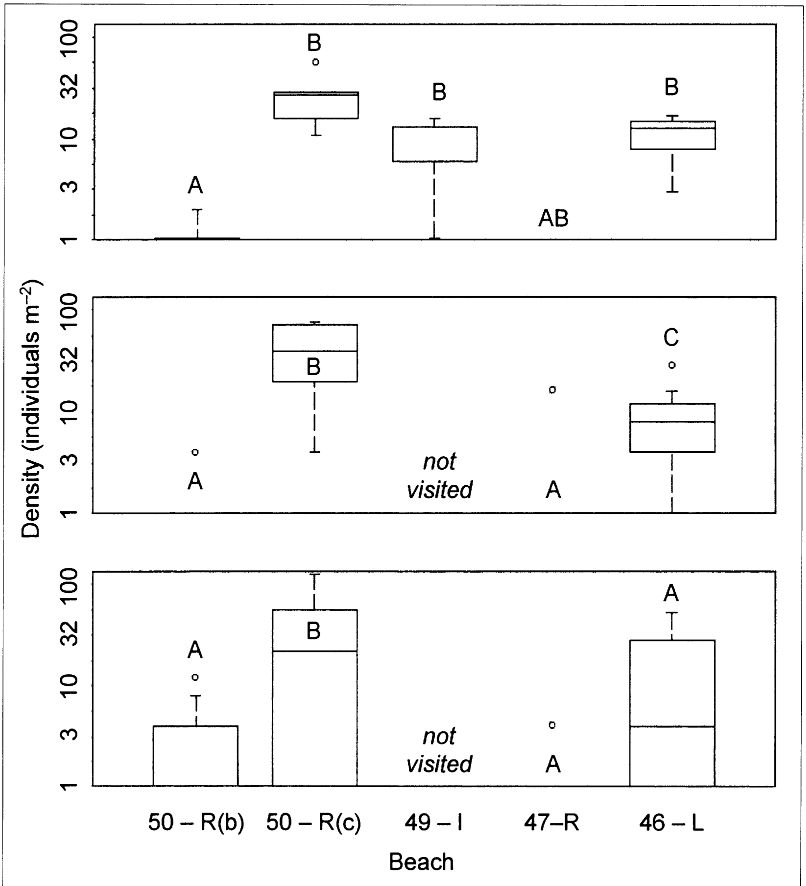


Figure 1. Density of larvae at five beaches on three dates. Top: 7–8 Oct 1999; middle: 6 Sept 2000; bottom 20 Sept 2000. Density did not differ significantly between beaches marked with the same letter (post–hoc pairwise Wilcoxon tests with Bonferroni correction). 49-I was only visited on the first date. Boxes show medians and quartiles, whiskers indicate data within 1.5 inter-quartile range of adjacent quartile, dots indicate outliers beyond that range.

ing for signs of recent use (e.g., footprints, vehicle tracks, fire scars, litter). In addition to verbal descriptions, I photographed each beach from a number of angles. Finally, I opportunistically noted the presence of other insect species, or collected specimens for identification.

RESULTS

Larval habitat description

Larval density was significantly different among the five beaches (Kruskal-Wallis tests, 7–8 Oct 99: c24 = 26.0, $p < 0.001$; 6 Sept 00: c23 = 34.3, $p < 0.001$; 20 Sept 00: c23 = 15.0, $p < 0.002$). Although there were subtle differences among the three sample dates, in general, density was significantly higher at 50-R(c), 49-I, and 46-L than at 50-R(b) and 47-R (Fig. 1). The beaches also differed in sand texture (Fig. 2). The correlation between sand texture (median of component 1 from PCA) and larval density ($\log_{10}(y)$) was 0.88, 0.78, and 0.74 on the three dates respectively.

Similar results emerged from the intensive study at 50-R(b) and 46-L. In general, density of larvae was higher near the top of the beaches (Fig. 3). To control for differences in transect length (50-R[b] was 9–14m wide, 46-L was 4–6m wide), I analyzed the density of larvae within a 2 m X 2 m quadrat at the point in each transect where density was

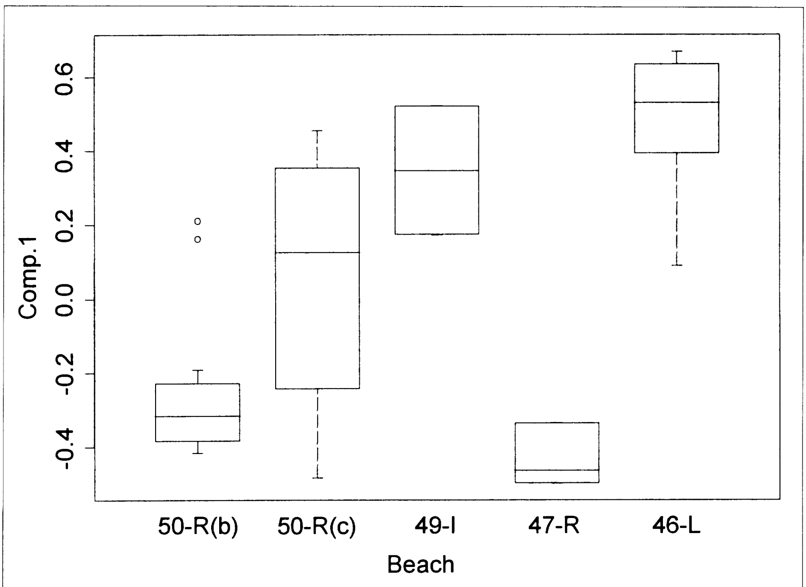


Figure 2. Sand texture represented by component 1 from PCA of samples from the same five beaches depicted in Fig. 1. Symbology as in Fig. 1. Outliers from 50-R (b) were from areas with turf and consequently a significant proportion of fine organic particles.

greatest (i.e., centered at the peak for each line in Fig. 3). Results were similar when I analyzed total density within transects.

In the multiple regression analyses, I found that residuals more nearly matched a normal distribution if I analyzed $\log_{10}(y)$. There were no influential outliers. With texture represented by the fractions of particles in each of five size classes, AIC favored selection of a model that included the fraction of very fine particles at the surface and the fraction of coarse particles at the surface (Table 1). Both slope parameters were negative, indicating that larvae were denser where there were fewer very fine and coarse particles. Similar analysis with texture represented by PCA scores led to a model with one term, component 2 of surface sand texture. Component 2 was subparallel with the fraction of fine particles (negatively correlated) and the fraction of very fine particles (positively correlated). The slope parameter was negative, indicat-

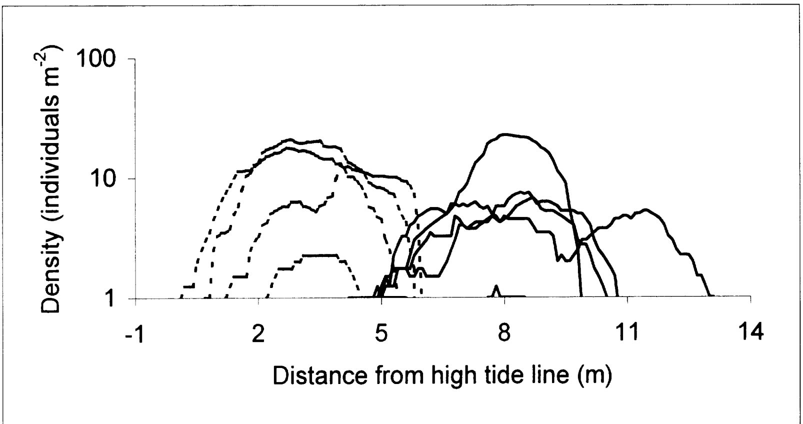


Figure 3. Density within 2 m X 2 m sliding quadrats along each of the transects. Transects at 46-L are shown with dashed lines (N = 4) and transects at 50-R(b) are shown with solid lines (N = 7).

Table 1. Model selection for multiple regression analyses. Top: sand texture represented by proportions of particles in five size classes; bottom: sand texture represented by the first two principal components of the proportions.

Model	Residual SS	AIC
intercept	2.80	3.36
intercept + surface—very fine	1.99	3.11
intercept + surface—very fine + surface—coarse	0.89	2.57
$R^2 = 0.68$, $F_{2,8} = 8.54$, $p = 0.01$		
intercept	2.80	3.36
intercept + surface—comp.2	1.69	2.81
$R^2 = 0.40$, $F_{1,9} = 5.88$, $p = 0.04$		

ing that there were more larvae where the fraction of fine particles was larger and the fractions of very fine particles was smaller (Fig. 4). The model that included the fraction of very fine and coarse particles had a lower AIC than the model with surface sand texture represented by component 2, and it explained more of the variation in the data (Table 1). The latter model, however, was superior to any other one-term model from either set of candidate models. Terms representing sand texture 30 cm below the surface, sand moisture, whether at or below the surface, cover, or prey availability were not included in the favored models, nor were terms representing the fraction of fine, medium, or very coarse sand at the surface in the first analysis or component 1 at the surface in the second analysis.

I designated the three beaches where dense aggregations of larvae were found "model beaches" (50-R[c], 49-I, 46-L). The model beaches were sparsely vegetated beaches with fine to medium sand (particles predominantly 0.125–0.5 mm). They were adjacent to banks where woody plant growth was suppressed (e.g., by mowing or cultivation). The areas where dense aggregations of larvae were found were all less than 50 m long and about 2 m wide, although some of those areas are embedded within larger beaches.

Reintroduction site selection

I documented a total of 32 beaches between river km 111 and river km 24 (Table 2). The longest beach was the accreting spit on the left

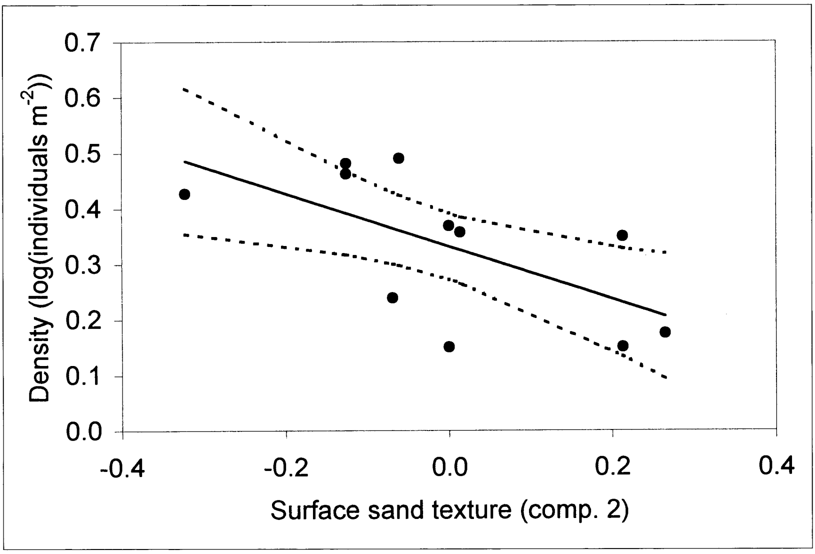


Figure 4. Density of larvae plotted over surface sand texture (represented by component 2); dots = measured density, solid line = regression model, dashed lines = 95% confidence interval of model.

bank at the Massachusetts-Connecticut state line (105-L) where there was a continuous sandy beach for about 700 m, but most were much smaller; only six beaches were longer than 100 m. In addition, most beaches were narrow; only four of the beaches were 20 m wide or wider. Finally, most beaches were within 1 km of another beach, and 14 were within 0.5 km of the nearest neighbor (Fig. 5a). Only nine beaches had two or more other beaches within 1 km, but 17 had two or more neighbors within 2 km (Fig. 5b).

The majority (20 of 32) of the beaches on the surveyed stretch of the river was nearly unvegetated. Similarly, the majority (20 of 32) was next to unforested banks, and most (20 of 32) were little used recreationally. However, those three conditions did not always co-occur. Half of the little-used beaches had significant plant growth mixed with patches of open sand (10 of 20), and more than half of the beaches

Table 2. Beaches between river km 113 and 24 indexed by river km and bank (L = left bank, I = island, R = right bank). Classification of sand texture based on cluster analysis except in a few cases where it was based on description in field notes indicated by square brackets. * indicates *C. puritana* adults and larvae have been seen at the site, + indicates that only adults have been seen. N = neighbor, NN = nearest neighbor, Recr = recreation.

Beach	Town	Sand texture	Size (m)	NN (km)	N w/i 1km	N w/i 2km	Plant Growth	Forest bank	Recr.	Date(s) visited
111-L	Longmeadow	fine	30X3	2.6	0	0	little	Yes	little	9/27/00
109-I	Longmeadow	med. w/ coarse	200X50	2.6	0	0	little	No	moderate	9/27/00
105-L (a)	Enfield	med. w/o coarse	700X50	4.0	0	0	moderate	Yes	little	9/27/00
105-L (b)		med. w/ coarse					little	No	heavy	
91-I	Windsor	fine	100X15	1.9	0	1	dense	Yes	little	7/23/00, 10/8/00
89-I	Windsor	med. w/o coarse	40X10	1.8	0	1	moderate	No	little	7/23/00, 10/8/00
87-I	Windsor	med. w/o coarse	30X10	1.8	0	0	little	No	little	7/23/00, 10/8/00
80-I	East Hartford	[silty]	50X1	0.2	1	1	moderate	No	little	7/14/99
80-R	Hartford	med. w/ coarse	100X20	0.2	1	0	little	No	little	7/14/99, 7/23/00
76-L	East Hartford	[silty fine sand]	100X10	3.5	0	0	little	No	moderate	6/24/99, 8/3/00
73-R	Hartford		50X1	0.3	2	2	little	Yes	moderate	6/24/99
72-R	Wethersfield		130X5	0.3	2	1	little	Yes	heavy	6/24/99
71-L	Glastonbury	med. w/o coarse	50X5	0.5	2	0	little	Yes	little	8/3/00
+ 68-R [1]	Wethersfield	med. w/ coarse	90X14	3.1	0	0	moderate	No	little	6/24/99, 8/3/00
65-L	Glastonbury		20X5	3.1	0	0	little	Yes	little	8/3/00
59-R	Rocky Hill		30X4	0.8	1	1	little	No	little	8/3/00
+ 58-R [2]	Rocky Hill	coarse	400X10	0.8	1	1	little	Yes	heavy	6/24/99, 8/3/00
56-R	Rocky Hill		30X2	1.3	0	1	moderate	No	heavy	7/12/99, 8/3/00
55-L	Glastonbury	med. w/o coarse	100X10	0.8	1	2	little	No	heavy	7/12/99, 10/5/00
54-R	Rocky Hill	[fine]	100X8	0.5	2	1	moderate	Yes	little	7/12/99, 7/23/99
+ 53-R	Rocky Hill	coarse	100X15	0.5	1	0	moderate	No	little	7/12/99, 7/23/99 10/5/00
+ 52-R	Cromwell	[fine]	80X7	0.3	2	4	little	Yes	little	7/12/99, 7/23/99
+ 51-R	Cromwell	[med. w/ coarse]	30X2	0.3	3	3	little	Yes	little	many
+ 50-L	Portland	[silty]	50X1	0.3	4	2	little	Yes	little	many
* 50-R (a)	Cromwell	med. w/o coarse	500X15	0.3	3	2	little	No	moderate	many
* 50-R (b)		med. w/ coarse					little	No	moderate	
* 50-R (c)		fine					moderate	No	heavy	
* 49-I	Portland	fine	50X5	0.3	2	2	dense	No	little	many
+ 48-I	Portland	[silty]	30X2	0.3	1	2	moderate	No	little	many
* 47-R [3]	Cromwell	med. w/ coarse	200X50	0.3	1	1	little	No	heavy	many
* 46-L	Portland	fine	80X5	1.3	0	0	moderate	No	little	many
42-L	Portland	coarse	80X12	3.5	0	0	little	No	little	9/30/00
39-I	Middletown		30X2	3.5	0	0	little	Yes	little	9/30/00
35-L	Haddam	med. w/o coarse	60X6	2.9	0	0	moderate	No	little	9/30/00
32-I	Haddam	med. w/ coarse	100X10	2.9	0	0	little	No	heavy	10/1/00

[1] single adult male seen 8/3/00. [2] adults previously reported by P. Nothnagle. [3] almost no larvae found on repeated visits despite large adult population.

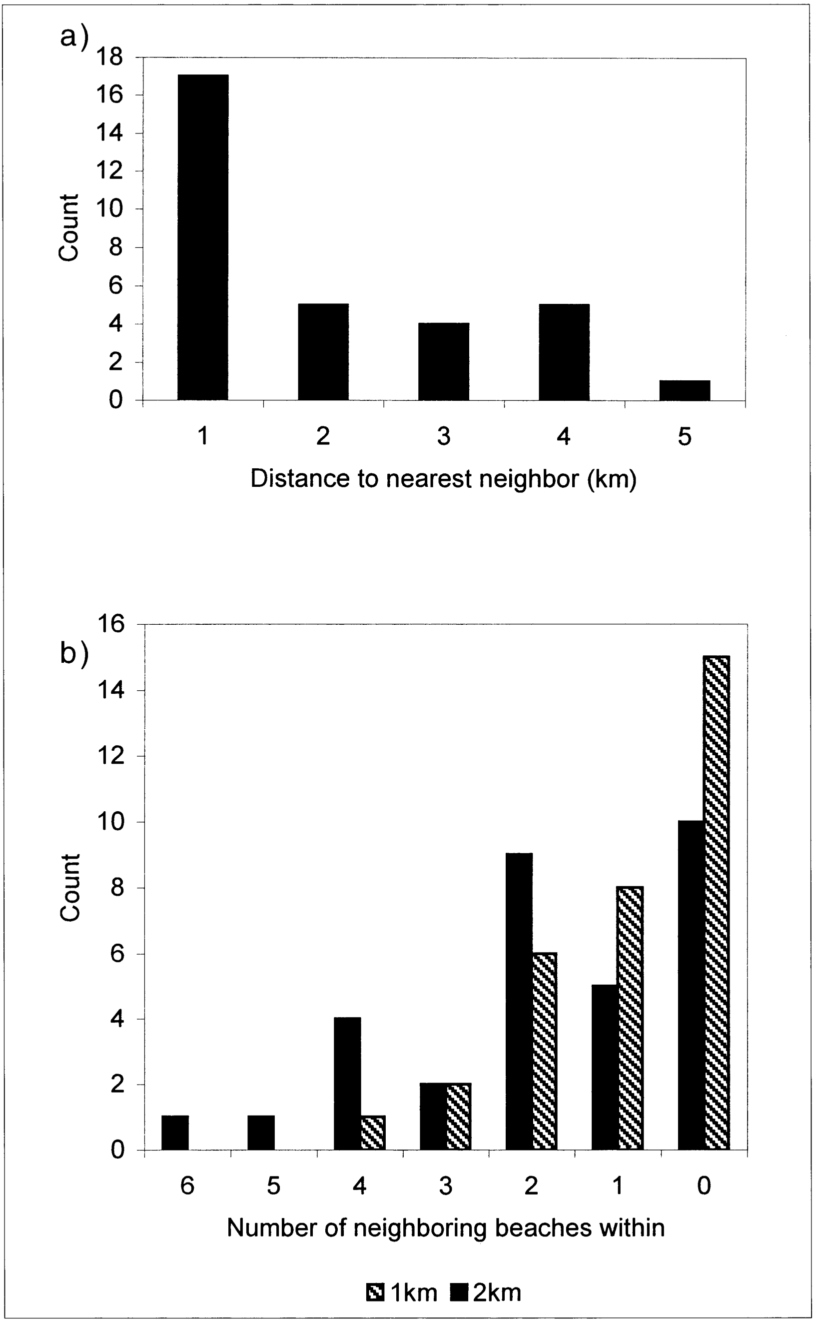


Figure 5. a) Histogram showing the number of beaches with the nearest neighboring beach within a given distance. b) Histograms showing the number of beaches with a given number of other beaches within one or two kilometers.

with significant areas of unvegetated sand were heavily or moderately used for recreation (11 of 20).

Sieve analysis clearly identified the sand samples from the model beaches (50-R[c], 49-I, and 46-L) as similar to each other, and clearly identified two other beaches as having the same type of sand. Cluster analysis (whether k-means, agglomerative, or divisive) grouped those three beaches together with beaches111-L and 91-I (Fig. 6a). Similarly, PCA showed those five beaches clustered together (Fig. 6b). Component 1 essentially differentiated sand samples on a gradient from medium (negative) to fine (positive) sand. Samples from beaches 50-R(c), 49-I, and 32-L all had high scores on component 1. The only other samples with similarly large component 1 scores were from beaches 111-L and 91-I.

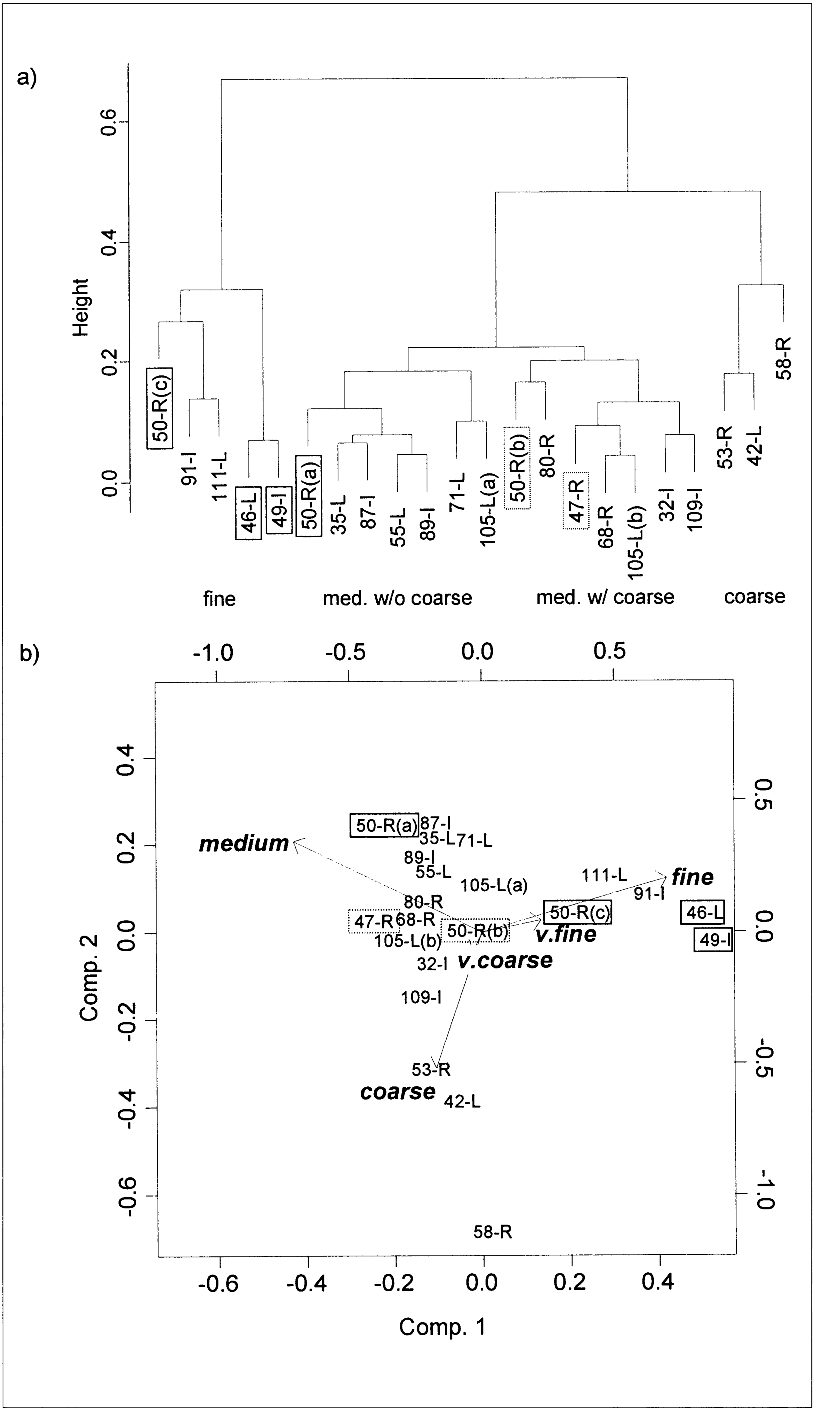
The majority of the other beaches had sand dominated by particles in the medium size class (Fig. 6). A small area of beach 50-R (subsection a) that also had a dense concentration of larvae had almost pure medium texture sand; I found similar sand at 89-I, 87-I, 55-L, and 35-L. A post-hoc classification based on the cluster analysis was made as indicated on Table 2 and Fig. 6a. Where I had field notes on sand texture but lacked data from sieve analysis, I included my field description in Table 2 (differentiated by brackets).

DISCUSSION

Larval habitat description

There are twelve beaches on the Connecticut River in the vicinity of Portland- Wethersfield, Connecticut where adult Puritan tiger beetles have been seen in the last ten years. However, few or no larvae have been found at many of those beaches. The beaches where dense aggregations of larvae have been seen are 50-R(c), 49-I, and 46-L. The quantitative samples reported here confirmed that those beaches have higher larval density than 50-R(b) or 47-R; it is worth noting that my estimates of larval density were low at 47-R despite the fact that I selectively placed quadrats where I saw some larvae or where the microhabitat appeared suitable. In addition, I visited three other beaches in the vicinity (55-L, 53-R, and 48-I) on days when many larvae were active at

Figure 6, facing page. a) Cluster diagram of sand texture from 22 of the beaches generated using the agglomerative hierarchical method. b) PCA biplot of the same 22 samples. Arrows indicate correlation of raw data (fraction of a sample in each of five particle size classes) with the first and second principal components. Labels were jiggled to reduce overlap, but relative positions were maintained. In both figures, solid outline = beaches with high density of larvae, dashed outline = beaches within river km 46–50 metapopulation with few larvae.


a)
Height
0.0
0.2
0.4
0.6
50-R(c)
91-I
111-L
46-L
49-I
50-R(a)
35-L
87-I
55-L
89-I
71-L
105-L(a)
50-R(b)
80-R
47-R
68-R
105-L(b)
32-I
109-I
53-R
42-L
58-R
fine
med. w/o coarse
med. w/ coarse
coarse
b)
-1.0
-0.5
0.0
0.5
Comp. 2
Comp. 1
-0.6
-0.4
-0.2
0.0
0.2
0.4
medium
fine
v.fine
v.coarse
coarse
50-R(a)
87-I
35-L
71-L
89-I
55-L
105-L(a)
111-L
91-I
80-R
50-R(c)
46-L
47-R
68-R
50-R(b)
49-I
105-L(b)
32-I
109-I
53-R
42-L
58-R
-1.0
-0.5
0.0
0.5

50-R(c) and 46-L, and I found no larvae despite extensive searching. I did not engage in the exercise of laying out quadrats in which I would have counted zero larvae, but those beaches could have been represented on Fig. 1 as having no larvae.

The most salient difference among beaches where I found many larvae and those where I found few larvae was the difference in sand texture, and the multiple regression analysis confirmed that sand texture mattered more than moisture, cover, or prey availability. Although that set of environmental variables may well be related, Puritan tiger beetles appeared to respond directly to sand texture more than to any of the other variables. Texture probably matters for ease of digging and maintaining burrows, as well as for burrow stability. Although there may be optimal soil moisture and temperature for Puritan tiger beetle larvae, the larvae can probably find their preferred moisture and temperature conditions in any of the soils in question given the range of available depths (many burrows were deeper than 50 cm). A rough idealized profile of their preferred sand texture based on that where density was highest would be 2 parts medium, 2 parts fine, and 1 part very fine particles.

In that light, it is interesting to note that the multiple regression analysis revealed that sand texture at the surface mattered more than sand texture 30 cm below the surface. When ovipositing, females may probe as deep as 1 cm, but they do not have direct access to information about the sand texture any deeper than that. Similarly, even if the larvae relocate from the site where the egg was laid, they would select a site based on what they can perceive at the surface. It should be noted that while a vertical profile through the beach sand reveals distinct strata at a fine scale reflecting depositional events, as a rule the sand 30 cm below the surface was quite similar to that at the surface.

It is particularly informative to look at the spatial pattern of both larval and adult densities at 50-R(c) and 50-R(b), which are adjacent but separated by a small tributary stream and riparian brush. Taken together, the entire beach was nearly 400 m long, but dense aggregations of larvae were found only in the 50 m stretch downriver of the inlet stream, here designated 50-R(c). Density of adults was also higher in that part of the beach, although it was high in the 20–50 m upriver of the inlet stream as well (pers. obs. and unpub. data, P. Nothnagle, Windsor, VT). Adult activity upstream of the inlet can be accounted for by their greater vagility; they may utilize adjacent habitat to forage but not to lay eggs.

Beyond sand texture, I characterized suitable habitat as being sparsely vegetated, but not unvegetated. Area should be at least 50 m X 5 m, and there should be other potentially suitable beaches within 1–2 km. Finally, the beach should be in an area where dynamism of the riverbank (deposition or erosion) is sufficient to prevent succession by woody plants, or where land use will suppress succession (e.g., mowing or cultivation).

Recommended reintroduction sites

The nearest apparently suitable patch to the extant metapopulation was 12 km downstream. Puritan tiger beetles move little among patches separated by distances of 1–3 km (Omland 2001), which suggests that there is little chance of regional expansion by natural colonization, at least on the time scale of decades. Therefore, the goal of establishing additional populations of Puritan tiger beetles on the Connecticut River must be approached by attempting to reintroduce the species to selected sites.

Taking into account similarities with the model beaches in terms of the classifications in Table 2, especially sand texture, an attempt to establish a new population of Puritan tiger beetles will have the best chance in the following areas (grouped as potential metapopulations).

Windsor Islands: Beach 91-I with 89-I, and 87-I

Beach 91-I is on one of a pair of islands in the center of the river channel on the Windsor-East Windsor town line. Apparently the slowing of the river there where it first encounters tidal influence favors the deposition of sediment and the formation of mid-channel islands, the dynamic movement of which maintains sparsely vegetated beaches. There is apparently suitable larval habitat on the southwest-facing shore of the upstream island, an area 100 m long and up to 15 m wide. There were also lower elevation areas elsewhere on the two islands that may be used by adults. The same island at river km 91 was selected in an earlier reintroduction attempt, which was unsuccessful because the translocated adults flew away (P. Nothnagle, unpub. report to Connecticut DEP, 1995). Future reintroduction attempts will involve translocating larvae, a tactic that has been used successfully with northeastern beach tiger beetles (*Cicindela dorsalis dorsalis* Say; Lane 1995, pers. comm., P. Nothnagle, Windsor, VT). The sand at beach 91-I is very similar to that at the model beaches. There is significant elevational relief on the beach, meaning that there would be a broad gradient of moisture conditions and inundation regimes from which beetles could select appropriate oviposition sites. The beach was quite free of vegetation when I was there on 23 July, although it was densely overgrown with *Polygonum pensylvanicum* when I was there on 8 October. Even amidst that rather dense plant growth, there were open patches of sand that could be occupied by Puritan tiger beetle larvae. There are areas of the model beaches that have nearly as dense plant growth and exceptionally dense concentrations of larvae.

Beach 91-I has the potential to form a metapopulation with two other beaches, 89-I, which is 1.9 km downstream, and 87-I, another 1.8 km beyond. My study of movement in the river km 46–50 metapopulation (Omland 2001) leads me to believe that beetles would occasionally fly among those islands. Those other two beaches are smaller, but still of a size that I believe could support a Puritan tiger beetle population. Although neither beach 89-I nor 87-I has as fine sand as the model beaches, both have medium sand similar to that in the small area of 50-R(a) where I also found a dense aggregation of larvae. All three of the beaches appeared to be little used recreationally in July, although there was a fire ring at beach 87-I in October.

Higganum Meadows: Beach 35-L

Beach 35-L in George Dudley Seymour State Park in Haddam, Connecticut is potentially a suitable habitat patch for Puritan tiger beetles. Sand samples from this beach were classified as medium texture with a small coarse fraction, also similar to that in the small area of 50-R(a) where there were many larvae. However, this beach is quite small and isolated. Furthermore, the nearest beaches (39-I, 4 km upstream and 32-I, 3 km downstream) did not appear to be suitable habitat. The beach is heavily overgrown with *Amorpha fruticosa*, a non-native invasive shrub, and encumbered with a heavy load of driftwood. The beach is little used by recreationalists (pers. obs., multiple visits in the summer 1999 as well as the visit in the fall of 2000).

The beach and adjacent grassland are state park lands that are already the focus of conservation interest. The grassland, known as Higganum Meadows, is classified as a floodplain terrace prairie, and is thought to be a globally unique ecological community (NatureServe 2001). The beach itself hosts a number of other noteworthy ground and tiger beetles including the only known population of *Nebria lacustris* in Connecticut or Rhode Island and two species of special concern (*Cicindela hirticollis* and *Tetragonoderus fasciatus*; unpub. data). *C. puritana* coexists with *C. hirticollis* and *T. fasciatus* on the beaches of the river km 46–50 metapopulation, and there are no reasons to expect that negative interactions (e.g., competition) among the species would detract from achieving multiple goals at the site. From that perspective, adding a Puritan tiger beetle reintroduction effort would fit well within the site's existing management goals.

Incidentally, although the sand at beach 111-L was more like that at the model beaches than the sand at beach 35-L, the former was only half the size of the latter, and it was heavily shaded by a canopy of trees, which would make it unsuitable for adult tiger beetles.

Conclusion

Establishing additional populations of Puritan tiger beetles is key to reducing the risk of losing the species from the Connecticut River region. At this point, the only strong source population on the whole river is the river km 46–50 metapopulation. Dispersal from that metapopulation is unlikely to lead to colonization of beaches farther upstream than river km 55 or farther downstream than river km 41. Therefore, establishing new populations elsewhere on the river will probably require translocation.

A reintroduction program is most likely to succeed where environmental conditions are suitable for the complete life cycle, but especially larval development. The best starting point for identifying such sites is resemblance to sites where larvae are known to occur at high density. I identified as model beaches three beaches in the river km 46–50 metapopulation where high larval density has been observed. I further identified beaches on three islands between river km 87–92 and a beach at river km 35 as the best candidates for a reintroduction attempt based on their resemblance to the model beaches. If a reintroduction program is undertaken, it should be viewed as an experiment in the context of adaptive management (Haney and Power 1996). Included in the agenda of the adaptive management program should be further refinement of habitat description for this species.

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