

Periodical cicadas use light for oviposition site selection

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Organisms use incomplete information from local experience to assess the suitability of potential habitat sites over a wide range of spatial and temporal scales. Although ecologists have long recognized the importance of spatial scales in habitat selection, few studies have investigated the temporal scales of habitat selection. In particular, cues in the immediate environment may commonly provide indirect information about future habitat quality. In periodical cicadas (*Magicicada* spp.), oviposition site selection represents a very long-term habitat choice. Adult female cicadas insert eggs into tree branches during a few weeks in the summer of emergence, but their oviposition choices determine the underground habitats of root-feeding nymphs over the following 13 or 17 years. Here, field experiments are used to show that female cicadas use the local light environment of host trees during the summer of emergence to select long-term host trees. Light environments may also influence oviposition microsite selection within hosts, suggesting a potential behavioural mechanism for associating solar cues with host trees. In contrast, experimental nutrient enrichment of host trees did not influence cicada oviposition densities. These findings suggest that the light environments around host trees may provide a robust predictor of host tree quality in the near future. This habitat selection may influence the spatial distribution of several cicada-mediated ecological processes in eastern North American forests.

Keywords: indirect cues; underground habitat selection; light environment; oviposition site selection; nutrient enrichment; periodical cicadas (*Magicicada* spp.)

1. INTRODUCTION

Since opportunities for direct habitat assessment are limited, organisms often use indirect cues to assess the quality of potential habitat sites (Orrians & Wittenberger 1991; Kokko & Sutherland 2001; Schlaepfer *et al.* 2002; Stamps & Krishnan 2005, and references therein). Indirect cues provide information about the aspects of habitat quality that cannot be evaluated directly owing to constraints of time, effort, risk or phenology (Stamps 1987; Orrians & Wittenberger 1991; Kokko & Sutherland 2001; Schlaepfer *et al.* 2002; Stamps & Krishnan 2005). In particular, many organisms may use indirect cues that reflect the spatial and temporal scales of their expected habitat association. Although ecologists have long since recognized the importance of spatial scales in habitat selection (e.g. Pulliam & Danielson 1991; Kristan 2003), few studies have investigated the temporal scales of habitat selection.

In dynamic systems, indirect cues in the immediate environment can provide information about future habitat quality. For example, female yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) appear to use aquatic insect emergence during a brief settlement period to assess future prey availability during the subsequent summer breeding season (Orrians & Wittenberger 1991). Despite the patchy and dynamic nature of the emergence of insects

in this system, early cues provide sufficient information to predict substantial variation in prey availability at scales relevant to seasonal blackbird foraging (Orrians & Wittenberger 1991).

Cues of future habitat quality may be particularly relevant for organisms with relatively sessile life stages. For example, many marine invertebrates (Grosberg 1981; Qian 1999), such as amphibians (Rudolf & Rödel 2005), galling insects (Price *et al.* 1987) and plants (Bazzaz 1991), commit to long-term habitat sites with incomplete information. While the time-scales of habitat associations vary widely across diverse systems, cues of future habitat quality may be an important general component of habitat selection behaviour in many systems.

In periodical cicadas, oviposition site selection represents an extremely long-term habitat choice. Adult female periodical cicadas (*Magicicada* spp.) insert eggs into shallow incisions on 3–11 mm diameter woody shoots during 2–3 weeks in the summer of emergence (White 1980; Oberdorster & Grant 2006; see electronic supplementary material A). The location of periodical cicada oviposition determines where the next generation of nymphs will hatch and fall, dig for host roots, feed on plant xylem, develop underground for 13 or 17 years and eventually emerge as adults (Marlatt 1907). Cicada nymphs are relatively sessile underground, generally travelling only few centimetres over the course of 13 or 17 years (White & Lloyd 1975; Maier 1980). Although cicada nymphs can select between the nearby host roots, their underground tunnels are short—approximately five times their body length over most of the nymphal stages

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(White & Lloyd 1975)—with larger tunnels to the soil surface constructed only by fifth instar nymphs in the months before emergence (Maier 1980). Periodical cicadas have the longest development of any known insect (Williams & Simon 1995), and the oviposition of adult cicadas determines the long-term habitats of these underground nymphal stages on larger scales (Marlatt 1907; Oberdorster & Grant 2006). Owing to their limited mobility and long host association, periodical cicadas exemplify a ‘parasite’ (rather than a ‘grazer’) strategy (Thompson 1988), in which the oviposition decisions of the adult female are expected to be especially important for future offspring fitness.

Periodical cicadas provide a particularly apt system for investigating indirect cues of future habitat quality. Adult cicadas are both spatially and temporally limited in their ability to assess the habitat quality of nymphs. Ovipositing cicadas cannot directly assess underground habitats or evaluate aboveground cues at the temporal scale of nymphal development. Previous studies suggest that cicadas use multiple indirect cues at multiple scales to select oviposition sites (Oberdorster & Grant 2006). Most cicadas disperse less than 50 m (Karban 1981), and courtship, mating and oviposition often occur near the natal site (Cook *et al.* 2001; Oberdorster & Grant 2006). This natal philopatry may reflect a strategy for selecting proven successful habitats. However, mated females occasionally make longer dispersal flights to colonize new habitats (Karban 1981; Lloyd *et al.* 1982), and they also actively discriminate between tree hosts for oviposition at smaller scales. For example, cicadas avoid ovipositing in resinous conifers (White *et al.* 1982) and may favour some hardwood species over others (Forsythe 1976; White 1980; Cook *et al.* 2001).

More generally, several observations indicate that cicadas preferentially aggregate on younger or faster growing trees, often along roadsides or forest edges, in suburban areas and early successional forests (White *et al.* 1979; White 1980). Other observations suggest that underground nymphal growth and survival may be maximized on the roots of rapidly growing host trees (White & Lloyd 1975; White *et al.* 1979). For example, fertilized orchards support greater cicada densities and larger individuals than populations from adjacent forests (Hamilton 1961; Maier 1980; White & Lloyd 1985). Underground heterogeneity in root availability within natural forests has also been suggested as a factor causing variation in the density and size of cicada nymphs (White & Lloyd 1975; Maier 1980; Rodenhouse *et al.* 1997). For example, Maier (1980) observed that fourth and fifth instar cicada nymphs are denser in areas of greater root density. Long-term habitat factors that influence the survival and size of cicadas may have direct effects on fitness: larger female cicadas are able to produce more eggs (Brown & Chippendale 1973), and larger male cicadas are more successful in courtship and mating (Karban 1983). These patterns are consistent with the plant vigour hypothesis (Price 1991), which suggests that herbivores often prefer to feed on vigorous plants, especially in close plant–herbivore interactions, where the effects of induced plant defences are minimal, such as xylem-feeding periodical cicadas (Williams & Simon 1995).

Although ecologists have observed intriguing patterns of habitat selection in cicadas, this study presents a novel

experimental approach to investigate the proximate cues and behavioural mechanisms of cicada habitat selection. In particular, both the fertilization and local light environments of host trees have been suggested as proximate cues for habitat selection (White 1980; Maier 1982). Both factors appear to be plausible cues of habitat quality. Fertilization rapidly increases the nitrogen content of xylem in a wide range of woody and herbaceous plants (Tromp & Ovaas 1985; Rossi *et al.* 1996; Youssefi *et al.* 2000). Since plant xylem contains approximately 99.9% water (White & Strehl 1978; Mattson 1980), cicadas and other xylem feeders show adaptations for assimilating nitrogen from this dilute source (White & Strehl 1978; Mattson 1980; Rossi *et al.* 1996). Several non-cicada xylophagous insects have shown an ability to detect differences in the nitrogen content of xylem in potential hosts, a preference for feeding on plants with higher nitrogen content in xylem and increased growth on fertilized plants (Rossi *et al.* 1996; Brodbeck *et al.* 1999, 2004). Nymphal periodical cicadas appear to ‘count’ seasonal cycles underground using fluctuations in the quality of host xylem fluid (Karban *et al.* 2000), suggesting that they are able to distinguish differences in xylem nutrient concentrations. Similarly, adult female cicadas often feed during oviposition (see electronic supplementary material A) and they may evaluate the nutrient status of potential hosts by sampling plant xylem (White 1980; Maier 1982). Several authors have noted that the size and density of cicada nymphs appear to be greater on the roots of fertilized trees (Maier 1980; White & Lloyd 1985; Williams & Simon 1995).

The light environment around host trees may also be an important cue of habitat quality for cicadas. For example, crown exposure is a very strong predictor of long-term growth for hardwood trees (Cole & Lorimer 1994), and red oak saplings respond to experimental canopy gaps with increased growth, especially in root biomass (Naidu & Delucia 1997). These observations suggest that the light environment of trees may be an important predictor of the habitat quality of underground cicada over longer time-scales. Adult cicadas are known to regulate their body temperature using behavioural responses to sunlight and shade (Heath 1967) and preferentially aggregate for courtship on sunlit forest edges and taller trees (Dybas & Lloyd 1974; White *et al.* 1979; White 1980; Karban 1981; Williams *et al.* 1993; Rodenhouse *et al.* 1997; Oberdorster & Grant 2006). Previous observations suggest that solar warming may be important for cicada flight, chorusing and oviposition behaviour (Maier 1982; Williams & Smith 1991; Moore *et al.* 1993). These observations suggest that ovipositing cicadas are capable of assessing both light and nutrient cues, but do not indicate whether either of these factors is actually used for oviposition site selection. Since light and nutrient heterogeneity often occur together and both factors co-occur with many other uncontrolled factors in natural tree populations, an experimental approach allows stronger inference to evaluate light and nutrient status separately as potential mechanisms of long-term habitat selection.

In this study, two hypothesized indirect cues for oviposition site selection are investigated. (i) How does the nutrient status of potential host trees influence habitat selection in cicadas? (ii) How does the local light environment around potential host trees influence habitat

selection in cicadas at between-host and within-host scales? More generally, this study investigates how individuals use the features of the immediate environment to choose future habitats.

2. MATERIAL AND METHODS

(a) *Between-tree habitat selection*

A field experiment coordinated to the 2004 emergence of Brood X 17-year periodical cicadas was conducted to investigate the effects of host tree nutrient and light environments on long-term habitat selection in periodical cicadas. Thirty two three-year-old red oak (*Quercus rubra*) trees (mean height \pm s.d., 118 ± 21 cm; mean diameter at 50 cm, 7.9 ± 1.6 mm) were planted along a 96 m transect (at 3 m intervals) through a 16-year-old successional forest and gap mosaic ($39^{\circ}3'42.99''$ N $78^{\circ}4'27.19''$ W) at the Blandy Experimental Farm (University of Virginia) on 4 April 2004. The order of trees along this transect was randomly assigned and the trunk diameters of these experimentally planted trees were within the preferred range for cicada oviposition. The surrounding habitat was characterized by a heterogeneous mixture of trees, shrubs, grasses and forbs of varying ages, including black walnut (*Juglans nigra*), honey locust (*Gleditsia triacanthos*), tree-of-heaven (*Ailanthus altissima*), black locust (*Robinia pseudoacacia*), mockernut hickory (*Carya tomentosa*), buckthorn (*Juglans cinera*), blackberry (*Rubus* spp.), oriental bittersweet (*Celastrus orbiculatus*), tall goldenrod (*Solidago altissima*) and tall fescue (*Festuca elatior*). This location was chosen to reflect an ecologically relevant cicada oviposition habitat at the landscape scale, while maintaining natural heterogeneity in local light environments around each tree. Red oak is a common native species in this forest and a common oviposition host of periodical cicadas (Williams & Simon 1995). Importantly, this transect location was not forested during the previous emergence in 1987, and this early successional forest experienced very low (fewer than four cicadas per square metre) emergence of cicada densities in 2004. Since very few cicadas emerged at the transect site, all the cicada ovipositions are assumed to be a result of active oviposition site selection by recently immigrated cicadas. Colonization of early successional forests and forest gaps appears to be a common pattern of periodical cicada behaviour (White *et al.* 1979; White & Lloyd 1985; Rodenhouse *et al.* 1997) and may be increasingly common in fragmented forests. In late May 2004, the transect and surrounding successional forest were naturally colonized by adult periodical cicadas (94% *Magicalcicada cassini* and 6% *Magicalcicada septendecim*) from several populations less than 0.5 km distant. The transect path was approximately 20–40 m from the southeastern edge of an over 90-year-old forest stand, which experienced low cicada emergence densities (mean, 11.4 cicadas per square metre; s.d., 14.9) in 2004. Owing to the well-documented forest history at this location, this experimental transect provided an uncommonly good opportunity to investigate the habitat selection behaviour of periodical cicadas colonizing new forest habitats without the historical effects of prior local emergence.

Experimental trees were assigned to alternating nutrient-enriched control groups after randomization of the first tree in the series. This systematic approach was favoured to maximize interspersed treatment groups (Hurlbert 1984). Each nutrient-enriched tree was given one slow-release fertilizer spike (Miracle-Gro Tree and Shrub Fertilizer Spikes) immediately after planting (4 April 2006) and

biweekly supplements of fertilizer solution (Miracle-Gro All Purpose Plant Food) during the active growth season between 5 May 2004 and 30 June 2004. Previous studies have shown that nitrogen concentrations of xylem in several woody trees increase rapidly (within 1–39 days) in response to fertilization (Crafts & Broyer 1938; Tromp 1983; Tromp & Ova 1985; BassiriRad *et al.* 1999; Youssefi *et al.* 2000). The first evidence of the emergence of cicadas was observed at this site on 15th May, with the vast majority of cicadas emerging by 22nd May. Most oviposition occurred between the end of May and mid-June.

In this study, light is defined as incident solar radiation, including the visible, ultraviolet and infrared portions of the electromagnetic spectrum. The light environment above each experimental tree was measured by the analysis of hemispherical canopy photographs (Comeau *et al.* 1998). Hemispherical (180°) photographs were taken using a vertically oriented Nikon Coolpix 995 digital camera with a Nikon FC-E8 fisheye lens converter. These photographs were analysed using the GAP LIGHT ANALYZER (GLA) v. 2.0 (Frazer *et al.* 1999) software to determine the proportion of visible sky ('percentage of canopy openness') and the fraction of solar radiation above the canopy that is transmitted to the forest understorey ('percentage of transmitted light') above each experimental tree. Canopy openness is an attribute of the canopy gap structure, while indices of transmitted light also incorporate global location and local seasonal solar radiation data. The GLA v. 2.0 software was parameterized with 30-year monthly averages of solar radiation data from the Weather Bureau Army Navy monitoring station in Sterling, VA ($38^{\circ}57'0''$ N $77^{\circ}27'0''$ W). The observed variation in canopy openness and solar radiation among trees resulted from the heterogeneous structure of this successional forest, which included a complex mosaic of trees, grasses and herbaceous vegetation of widely varying ages and heights. The light environment of individual trees was largely affected by the size and the structure of the neighbouring vegetation on a local scale (1–5 m). By utilizing this natural variation in light availability, this study combines a manipulated factor (nitrogen availability) with a mensurative factor (light), *sensu* Hurlbert (1984).

Cicada oviposition leaves a readily visible, persistent and diagnostic scar on the surface of the trees (Marlatt 1907). Cicada oviposition density on experimental trees was measured as the number of eggnest incisions per square centimetre of tree surface on 30 June 2004 after the completion of cicada oviposition. All eggnest incisions on tree trunks and lateral branches of the between-tree experiment were counted. The structure of these trees was generally columnar; leaves emerged apically or from short (usually less than 30 cm), sparse (usually less than three branches per plant) and thin (usually less than 4 mm diameter) lateral branches. Owing to this architecture, tree surface area was approximated as a cylinder of measured tree height and diameter at 50 cm. Analyses using linear density (incisions per unit height) and absolute counts of oviposition incisions per tree yielded identical conclusions. Each eggnest incision represents an investment of 20–30 eggs (Williams & Simon 1995), and the density of eggnest incisions provides a useful relative measure of oviposition habitat preference in periodical cicadas (White 1980).

Two general linear model analyses were conducted to investigate the effects of nutrient enrichment, light environment and the nutrient–light interaction. Separate analyses

were conducted to include both measures of the light environment (canopy openness and transmitted light). Since measures of canopy openness and transmitted light are highly correlated in this dataset ($R_{\text{adj}}^2 = 0.95$) and all analyses yielded identical conclusions with both measures, only the results of the canopy-openness analyses are shown in figure 1a. Cicada oviposition density was square root-transformed prior to regression to meet the assumptions of residual normality (Shapiro–Wilk's $W_{\text{canopy}} = 0.96$, $p = 0.42$). These data met assumptions of homogeneous variances between nutrient enrichment groups (Levene's test, $p = 0.43$). In order to investigate the relationship between light environments and between-tree habitat selection in cicadas, linear least square regressions were fit to scatterplots of oviposition densities against canopy openness. Since cicadas avoid placing eggnefts near other eggnefts at high densities (White 1980), potential interactions among ovipositing females are likely to produce conservative analyses that favour null hypotheses.

(b) *Within-tree habitat selection*

A second experiment was conducted using the same experimentally planted tree transect to investigate the proximate effects of within-tree microenvironments on oviposition site selection in periodical cicadas. The specific hypothesis was that cicada oviposition would be greatest on the southern aspect of tree trunks with the greatest direct solar exposure. The directional bearing of oviposition scars around the circumference of vertical trunks for each experimental tree was measured. Each oviposition scar represents a series of eggneft incisions oviposited by a single female. Oviposition scars on lateral branches were excluded from this within-tree census to minimize the effects of existing tree architecture on the directional distribution of oviposition microhabitats (see also Cook *et al.* 2001); owing to the sparseness and small diameter of these branches, relatively few oviposition scars were present on lateral branches. The vertical trunks of all the experimental trees were within the range of diameters suitable for oviposition (White 1980) and provided a uniform, natural and interpretable arena for investigating the directional bearings of oviposition sites.

A Rayleigh test was used to investigate the overall mean bearing (a_{overall}) and angular concentration (ρ_{overall}) of oviposition scars across all trees (Zar 1999). The Rayleigh test evaluates the specific hypothesis of a uniform circular distribution ($H_0: \rho = 0$) against the alternative of a significant mean direction ($H_1: \rho \neq 0$). Additionally, the mean bearing (a_i) and angular concentration (ρ_i) of oviposition scars were calculated separately within each tree i . The grand mean (a_{grand}) was calculated as the second-order mean of the tree mean bearings weighted by ρ_i , and its significance was evaluated with Hotelling's procedure (Zar 1999). A 95% confidence interval (CI) for the grand mean was determined from the second-order means (Zar 1999).

3. RESULTS

Periodical cicada oviposition densities were not affected by nutrient enrichment of host trees (see electronic supplementary material B, $p = 0.72$) or the nutrient–light interaction ($p = 0.55$). However, the light environment of host trees had a strong positive effect on cicada oviposition density (figure 1a, $p < 0.0001$). Cicada oviposition density increased rapidly with increasing canopy openness

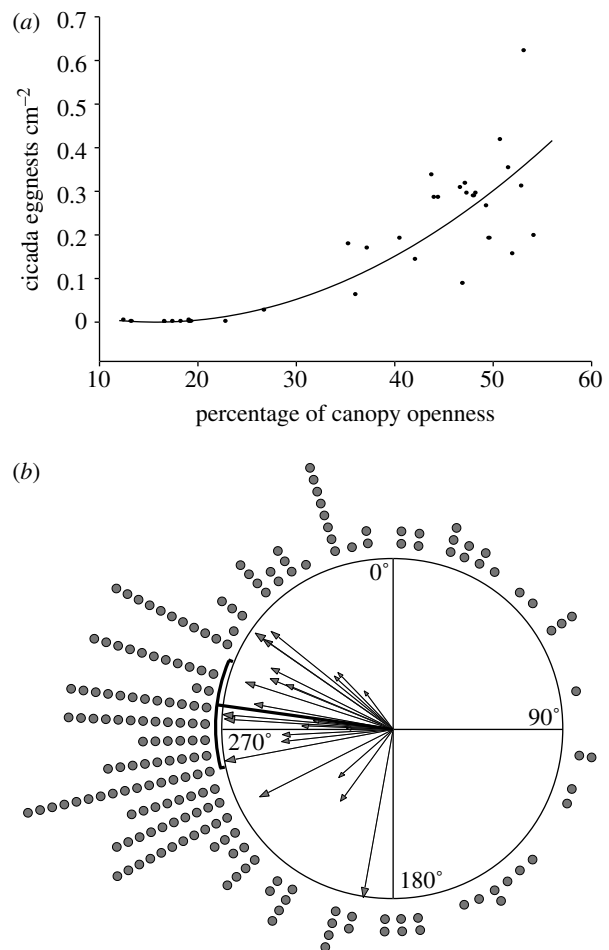


Figure 1. (a) Cicada oviposition (eggneft incision) density is greater on trees with greater light exposure. The solid line represents a fitted regression of square root-transformed oviposition density against canopy openness (back-transformed). (b) Oviposition density is greater on the western aspect of tree trunks. External circles represent the bearings of 189 oviposition scars on vertical tree trunks. Vectors indicate the mean bearings of oviposition scars on 23 trees. The length of each vector indicates the concentration of data for each tree mean. The bold line represents the grand mean angle and the external bracket represents 95% CI for the grand mean.

(figure 1a, $R_{\text{adj}}^2 = 0.86$, $p < 0.0001$) in regression analyses. Trees in local environments with less than 25% canopy openness experienced extremely rare cicada oviposition, while high oviposition densities were common in high light environments (figure 1a).

Cicadas preferentially oviposited on the western aspect of tree trunks (figure 1b). This result was consistent and significant for both the overall mean bearing among all oviposition scars ($a_{\text{overall}} = 273.0^\circ$, $\rho_{\text{overall}} = 0.583$, $p < 0.05$) and for the weighted means among all trees ($a_{\text{grand}} = 277.1^\circ$, 95% CI: 256.8–293.8°). Eighty-two percent of all oviposition scars and the mean oviposition bearing for all the experimental trees occurred on the western hemisphere.

4. DISCUSSION

These results suggest that the solar radiation environment around host trees is a significant predictor of oviposition site selection by female periodical cicadas. In contrast, the nutrient environment of host trees did not influence

oviposition site selection. The immediate nutrient environment of a host tree may be a less informative long-term cue in dynamic nutrient environments, or cicadas may simply be unable to assess the cues of nutrient content of root xylem.

The observation of preferential oviposition on trees with greater canopy openness appears to be a strong and consistent pattern. This pattern suggests at least three non-exclusive adaptive mechanisms affecting adult performance, egg hatching success and nymphal development. First, adult female cicadas may prefer sunlit trees as oviposition sites owing to direct benefits during oviposition. For example, basking cicadas may be better able to evade predators or insert eggs owing to warmer body temperatures in sunlit environments, so that direct exposure to sunlight may indicate safer or more efficient oviposition sites. Several recent studies have illustrated that habitat selection may commonly reflect a combination of direct effects on adult females and indirect fitness effects via future offspring performance (Scheirs *et al.* 2000; Mayhew 2001; Henry *et al.* 2005). However, increased predator avoidance as a result of environmental thermoregulation seems unlikely to be an important factor in this system, as the overall *per capita* risk of predation for periodical cicadas is remarkably low owing to the strong effects of predator satiation (Karban 1983; Williams *et al.* 1993) and periodical cicadas are well-known for their weak predator avoidance behaviours (Lloyd & Dybas 1966).

Second, sunlit oviposition sites may improve egg development or hatching success. This appears to be a plausible explanation, though no data are available to directly investigate this mechanism. Previous studies indicate that host-species oviposition preferences do not correlate with hatching success (White 1980) and the effects of varying light environments have not been investigated. However, mortality at the hatching stage is very low—approximately 5% under natural conditions (Cory & Knight 1937) and 15% for cut branches in laboratory conditions (White & Lloyd 1981). Conversely, nymphal establishment underground is a particularly important stage for determining cicada fitness. By comparison, cicada mortality between egg hatching and the second year of nymphal development ranges between 42 and 98% (mean, 80%; Karban 1984, 1997).

A third possible explanation for the observed pattern of preferential oviposition on sunlit host trees is that the light environment of a host tree provides an indirect cue of underground habitat quality. Recently hatched nymphs are small (1–2 mm) and face the challenge of rapidly locating a suitable root to establish a feeding site. If open canopy environments generally have greater root density, the aboveground light environment may also provide an indirect cue of underground habitat quality. This mechanism is consistent with the observation that open canopy environments are known to be good predictors of long-term growth (Cole & Lorimer 1994) and rapid root development in hardwood trees (Naidu & Delucia 1997). This possibility would also be consistent with the plant vigour hypothesis (Price 1991) if the local light environment around host trees provides an indirect cue of the habitat quality of underground nymphs mediated through predicted tree growth and vigour.

These three alternative hypotheses suggest potential adaptive benefits at multiple points in the cicada life cycle,

including adult predator avoidance during oviposition, egg hatching success and nymphal establishment and growth. The results of this study cannot directly distinguish among these adaptive benefits, and these hypotheses are neither mutually exclusive nor exhaustive. However, periodical cicadas provide a unique opportunity to investigate hypothesized adaptive benefits across a wide range of temporal scales, and future studies may be able to evaluate the relative importance of these hypotheses directly. For example, the predator avoidance behaviour of adult females under shaded and sunlit conditions could be quantified using 'model predators' in a manner similar to Steward *et al.* (1988), and hatching success under a range of experimental light conditions could be measured using the methods of White (1980). Measurements of root densities and rates of nymphal establishment across natural gradients of light exposure may provide initial insights into the long-term suitability of underground habitat sites.

Finally, this pattern could result from a non-adaptive process. For example, variation in the light environment around host trees may be correlated with differences in the apparency of oviposition sites. Covariance between apparency and high light environments may commonly occur in natural systems, reinforcing these observed patterns of habitat selection.

Cicadas also showed a strong and consistent pattern of preferential oviposition on the western aspect of tree trunks. Though unexpected, these results suggest future investigations that may yield additional insights into the mechanisms of habitat selection in cicadas. The observed patterns suggest two *a posteriori* hypotheses: first, cicadas dispersing from the nearest mature forest may have encountered the western aspect of experimental trees first. This hypothesis seems less probable because cicadas were observed flying in many directions without apparent pattern throughout the complex structure of the 16-year-old successional forest (personal observation). Alternatively, the observed pattern of oviposition may suggest habitat selection for microsites within trees that have direct afternoon light exposure (see electronic supplementary material C). Although the greatest total light exposure generally occurs on southern aspects in Northern Hemisphere locations, periodical cicadas are generally inactive at body temperatures below 20°C (Heath 1967). As a result, most cicada oviposition occurs in the afternoon (Maier 1982), during peak daily temperatures. These results should probably not be interpreted to indicate that the different directional aspects present microhabitats of different host quality. These observations rather suggest the possibility that exposure to direct light provides a proximate cue for oviposition in periodical cicadas, indicating a potential behavioural mechanism by which cicadas can associate open light environments with particular host trees.

Together, these results provide experimental evidence indicating that light is an important predictor of habitat selection of cicada at between-host scales and may contribute to microsite selection at within-host scales. Light availability is an important habitat factor for many other insect herbivores, though the direction of these preferences is variable across systems (Bultman & Faeth 1988; Collinge & Louda 1988; Connor 2006). The variability of results in these studies may reflect the wide range of ecological mechanisms that are influenced by light

on short time-scales, including predation or parasitism risk, host quality and abiotic factors. However, the immediate light environments around a host tree may also provide information about future ecological conditions over considerably longer time-scales. Because cicadas oviposit on a broad range of taxa (White 1981), light may provide a particularly general and robust cue for habitat selection in the near future. Light cues may also contribute to observed host species preferences (White 1981; Cook *et al.* 2001; Oberdorster & Grant 2006) if the growth form of different host trees also influences their local light environment, or if different host species simply tend to occur in different light environments. These current results are also consistent with the observation that cicada oviposition densities are greater when trees are present at lower densities (Cook *et al.* 2001). This negative correlation between tree density and oviposition density has been interpreted as a 'dilution effect' resulting from the greater number of potential oviposition sites at higher tree densities (Cook *et al.* 2001). An alternative possibility suggested by these results is that areas of lower tree density may experience higher oviposition rates owing to greater light penetration.

These findings may contribute to larger questions about observed patterns of cicada distributions. Above-ground cicada distributions are notably patchy at a remarkably wide range of spatial scales (Dybas & Lloyd 1974; Williams & Simon 1995). The heterogeneity of cicada populations is likely to reflect a complex combination of historical and ongoing ecological processes: strong aggregation behaviours and limited dispersal at a proximate level (Karban 1981; Simon *et al.* 1981; Williams & Smith 1991; Oberdorster & Grant 2006) and Allee effects from a strategy of predator satiation at an ultimate level (Karban 1982b; Williams *et al.* 1993). Survival to emergence may represent a reliable cue of local habitat quality at a landscape scale if habitats are relatively unchanged on the time-scale of cicada generations. However, active habitat selection at *local* spatial scales allows cicadas to respond to habitat changes (e.g. forest growth or fragmentation). At these scales, the habitat decisions of ovipositing females and the survival of nymphs in the habitats selected determine the distribution of underground cicada populations, and oviposition decisions that contribute to successful nymphal establishment on underground roots would appear to be favoured by natural selection. In this sense, this habitat selection is an important behavioural bottleneck during a critical selective stage of the cicada lifecycle. In the fragmented and dynamic forests of eastern North America, the proximate cues used in local habitat selection may be increasingly important factors determining the distribution of cicada populations.

In many systems, habitat selection determines the context of individual interactions, affects the distribution and local abundance of populations, and influences the collective assembly and maintenance of communities and ecosystems. Since these decisions affect individual, population, community and ecosystem processes, ecologists have shown broad interest in both the consequences and the proximate mechanisms of habitat selection. In this system, the habitat selection behaviour of female cicadas is likely to influence the spatial distribution of three cicada-mediated ecological effects in North American forests: damage to host tree branches owing to accumulated

egg-nect incisions (Williams & Simon 1995), resource pulses of nutrients from dead cicada litterfall (Yang 2004, 2006) and long-term underground root herbivory by the subsequent nymphal generation (Karban 1980, 1982a). While the cumulative consequences of these effects are as yet unclear, these current findings suggest that local light environments during the summer of emergence may influence the long-term distribution and dynamics of these ecological processes, with substantially more persistent implications for these forest systems.

Periodical cicadas provide an extreme example of long-term habitat selection and may also suggest more general insights. First, these findings emphasize the importance of temporal scales in habitat selection. Many habitat selection decisions are likely to use both spatial and temporal cues, because habitat quality varies in both space and time. Second, habitat selection in periodical cicadas suggests that other organisms with relatively long, sessile life stages may be particularly likely to use indirect cues that predict future habitat quality. Third, this study suggests that environmental features operating on time-scales similar to the time-scale of an organism's habitat association may be the most informative predictors of future habitat quality. In complex and dynamic natural systems, these temporally indirect cues may be an important component of habitat selection behaviour.

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