Habitat loss is thought to be a cause of woodcock population declines, however little is known about the impact of exotic invasive vegetation on woodcock nest site selection and nesting success. In March and April of 2009 and 2010, we examined nest success and nesting habitat selection in relation to the abundance of exotic invasive vegetation at 13 nests in southeastern Pennsylvania. We used logistic regression and Akaike’s Information Criterion (AIC) to determine the best models for nest success and habitat use. Woodcock avoided exotic invasive vegetation when selecting nest sites. Nest success and habitat use decreased significantly with an increase in percentage of exotic invasive woody vegetation. Models containing percentage of exotic invasive woody vegetation were highly supported for nest success and habitat selection. We recommend that managers attempt to control and remove exotic invasive vegetation to promote increased woodcock nesting success and habitat use.

INTRODUCTION

American woodcock populations have experienced declines from 1968 to present (Sauer and Bortner 1991, Cooper and Parker 2010). These declines are thought to be linked to the degradation and decline of early successional habitats (Owen et al. 1977, Dwyer et al. 1983, Straw et al. 1994, Dessecker and McAuley 2001). Woodcock population trends in Pennsylvania are comparable to other eastern populations (Palmer 2008) and it may be reflective of the regional trend. Additionally, the importance of habitat components like singing grounds, feeding, nesting, and diurnal cover to woodcock survival has been studied in Pennsylvania (Liscinsky 1972, Kinsley and Storm 1988). Liscinsky (1972) reported that when one or more of these habitat components was missing, woodcock use declined rapidly. These studies documented the importance of native plant species like alder (Alnus spp.), crabapple (Malus spp.), hawthorn (Crataegus spp.) and dogwood (Cornus spp.) and recommended management on a shorter rotation that will allow habitat to remain in a young stage that is suitable for American woodcock (Liscinsky 1972, Gutzwiller 1980, Kinsley and Storm 1988). Previous research also concluded that woodcock had low selectivity for nesting site habitat, and utilized many different cover types (Mendall and Aldous 1943, Sheldon 1967, Liscinsky 1972, Coon et al. 1982). Adequate soil moisture is recognized as an important characteristic of woodcock feeding areas and is considered a limiting factor for woodcock habitat use, although previous research also concluded that drier, upland sites are typically used for nesting (Liscinsky 1972, Gregg and Hale 1977, Coon et al. 1982).

Exotic invasive vegetation (hereafter invasive vegetation or invasives) was not as prevalent during the time of previous studies as it is now, and little is known about the effect of invasive vegetation on woodcock nesting success and habitat use. Dense thickets of multiflora rose (Rosa multiflora), autumn olive (Elaeagnus umbellata), and tatarian honeysuckle (Lonicera tatarica) prevent native shrub and forb establishment and may be detrimental to nesting native birds (Luken and Thieret 1996, Hutchinson and Vankat 1997). These invasive shrubs have become common in southeastern Pennsylvania and are now listed as a serious threat because they out-compete native vegetation in the region (PADCNR 2009).

The Pennsylvania Game Commission’s Wildlife Action Plan (2008) identifies the management of early successional habitat as a high priority because of the decline in its quantity and quality. In Pennsylvania, the amount of forested acreage has not drastically declined in recent years (McWilliams 2007), but rather the forests have aged to a point that deters use by woodcock (Kinsley and Storm 1988). Moreover, the invasion of exotic shrubs is thought to influence native forest quality by reducing sunlight and soil nutrients available to native shrubs (Bratton 1982, Wilcove et al. 1998, Zavaleta 2000, Sala et al. 2000).

Woodcock have been listed as a species of greatest conservation concern in the Pennsylvania Wildlife Action Plan (PGC 2008), because they require early seral habitats (Men-
dall and Aldous 1943, Sepik et al. 1981). Given American woodcock population decline and encroachment of invasive vegetation, our objective was to determine whether invasive vegetation affects American woodcock nest success and nesting site selection. We hypothesize that American woodcock would show no preference for native vegetation over invasive and that nesting success would not differ between nest sites that contained native or invasive vegetation.

**MATERIALS AND METHODS**

**Study site.**

Our study was conducted at Swatara State Park near Suedberg in Lebanon and Schuylkill counties, in southeastern Pennsylvania (Fig. 1). The park is roughly 14 km² and lies in the Ridge and Valley Province (Bailey 1995). Dominant cover types include invasive shrublands, red maple (*Acer rubrum*) – elm (*Ulmus americana*) palustrine flood plains, red oak (*Quercus rubra*) – mixed hardwood forests, and northern hardwood forests (Fike 1999).

**Nest success.**

Singing ground surveys were conducted in early March of 2009 and 2010 by walking roads and hiking trails at dusk and listening for singing males. Singing grounds were identified using a Global Positioning System (GPS; Garmin, Olathe, KS).

Mist nets were strung across singing grounds to capture female woodcock who were visiting displaying males (Sheldon 1967) and trained pointing dogs (Ammann 1981) were used to locate nests in proximity to occupied singing grounds. For all woodcock captured, we recorded date, time, location of capture, capture method, bill length (mm), mass (g), and widths of outer 3 primary feathers (P10, P9, P8) measured 2 cm from the feather tip. Bill length, sum of P10 + P9 + P8 width measurements, and body mass were used to determine sex (Martin 1964).

All woodcock were fitted with United States Geological Survey leg bands. A 3 g radio transmitter (Model SOPB-2190, Wildlife Materials, Inc., Murphysboro, IL) was attached to all captured females using all-weather animal tag cement and a belly-loop wire harness (McAuley et al. 1993). Tracking of females began after release using a portable receiver and handheld yagi antenna (Wildlife Materials, Inc., Murphysboro, IL) to determine habitat used. When monitoring indicated that a female was in the same 0.5 ha area for 2 consecutive days, we located the bird visually to confirm nesting and recorded the number of eggs. Nests were checked remotely with binoculars every 3 days to verify their fate. If a signal was located in an area away from the nest, we visually determined the fate of the nest. We considered all nests that hatched ≥ 1 egg to be successful.

**Habitat composition.**

Two days after fledging or immediately following depredation or abandonment, we marked the location of each nest using a GPS, and recorded habitat composition in an 11.3 m radius plot (0.04 ha; James and Shugart 1970, McAuley et al. 1996) around the nest. Woody vegetation composition was measured by counting native and invasive woody vegetation stems ≥ 30.5 cm in height that emerged from the soil in the plot. Woody vegetation under 30.5 cm was omitted due to potential difficulty in identifying species without the presence of leaves. Soil moisture was measured using a RapiTest moisture meter with probe (Scherm et al. 1998; Luster Leaf Products, Inc., Woodstock, IL) that ranged from 0 for dry to 10 for wet. Soil moisture at each site was measured three times within 10 minutes and the average was calculated. Stem density was defined as the total number of native and invasive woody vegetation stems ≥ 30.5 cm tall within the plot divided by the plot area. Vegetation cover was obtained by dividing the number of invasive woody vegetation stems by the total number of woody vegetation stems found in the plot.

**Habitat selection.**

Habitat conditions between paired use and random locations were assessed for factors in nest site selection. Used sites were defined as nest locations and random sites were determined by randomly selecting a direction by flipping a coin twice (first for north or south and second for east or west) and then walking 70 m from the nest location in the combined direction. This distance was chosen to reflect the average distance that nests were found in relation to an occupied singing ground (Miller 2010).
Data analyses.

An information-theoretic approach (Burnham and Anderson 2002) was used to assess the importance of habitat covariates to woodcock nest success and habitat selection using logistic regression, based on models generated to reflect competing hypotheses. Relative support was then evaluated for these competing models using Akaike’s Information Criteria (AIC; Burnham and Anderson 2002). We developed a set of a-priori models to predict the effect of habitat variables on nesting success and nesting habitat use (Table 1). A Hosmer and Lemeshow (2000) goodness-of-fit test on the global model (Table 1) was conducted to determine whether it fit the observed values. Akaike’s Information Criterion adjusted for small sample size (AICc) and weight of evidence ($w_i$) were used to rank and select the most parsimonious models fit to the data (Burnham and Anderson 2002). We considered models with $\Delta_i \geq 2$ to have substantial support and models with $\Delta_i \geq 4$ to lack support (Burnham and Anderson 2002, Lloyd and Martin 2005). Student’s $t$-tests compared the means of normally distributed habitat variables recorded at paired nest and random sites. An Independent Mean test compared variables that were not normally distributed from successful and failed nests. All statistical analyses were performed using SPSS (Version 18, SPSS, Inc. 2009).

Table 1. Model selection results, bias-corrected Akaike’s Information Criterion (AICc), model weights ($w_i$), and parameters estimated ($K$) used to evaluate success of American woodcock nests in Swatara State Park, Schuylkill & Lebanon Counties, PA, USA during 2009–2010.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta_i$</th>
<th>$w_i$</th>
<th>$K$</th>
</tr>
</thead>
<tbody>
<tr>
<td>PER_INV</td>
<td>15.978</td>
<td>0.000</td>
<td>0.616</td>
<td>2</td>
</tr>
<tr>
<td>PER_INV + MOISTURE</td>
<td>18.862</td>
<td>2.884</td>
<td>0.146</td>
<td>3</td>
</tr>
<tr>
<td>NATIVE</td>
<td>20.210</td>
<td>4.232</td>
<td>0.074</td>
<td>2</td>
</tr>
<tr>
<td>STEMDENs</td>
<td>21.138</td>
<td>5.160</td>
<td>0.045</td>
<td>2</td>
</tr>
<tr>
<td>MOISTURE</td>
<td>21.248</td>
<td>5.270</td>
<td>0.044</td>
<td>2</td>
</tr>
<tr>
<td>INVASIVE + MOISTURE</td>
<td>21.977</td>
<td>5.999</td>
<td>0.031</td>
<td>2</td>
</tr>
<tr>
<td>INVASIVE</td>
<td>22.052</td>
<td>6.074</td>
<td>0.030</td>
<td>2</td>
</tr>
<tr>
<td>NATIVE + MOISTURE</td>
<td>23.665</td>
<td>7.687</td>
<td>0.013</td>
<td>3</td>
</tr>
<tr>
<td>GLOBAL</td>
<td>36.160</td>
<td>20.182</td>
<td>0.001</td>
<td>6</td>
</tr>
</tbody>
</table>

$\text{PER_INV}=\text{percentage of invasive stems present in 0.04 ha circular area around each nest.}$

$\text{MOISTURE}=\text{amount of moisture measured in soil with a RapiTest soil meter; 0 = dry, 10 = wet.}$

$\text{NATIVE}=\text{number of native stems} \geq 30.5\text{ cm within 0.04 ha circular area around each nest.}$

$\text{STEMDENS}=\text{density of woody vegetation} \geq 30.5\text{ cm in height} /\text{m}^2.$

$\text{INVASIVE}=\text{number of invasive species} \geq 30.5\text{ cm present within 0.04 ha circular area around each nest.}$

$\text{GLOBAL}=\text{contains all measured variables.}$


<table>
<thead>
<tr>
<th>Variablea</th>
<th>$\beta$</th>
<th>SE</th>
<th>Odds Ratio</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>NATIVE</td>
<td>0.014</td>
<td>0.011</td>
<td>1.015</td>
<td>0.993 to 1.037</td>
</tr>
<tr>
<td>MOISTURE</td>
<td>0.006</td>
<td>0.006</td>
<td>1.006</td>
<td>0.999 to 1.013</td>
</tr>
<tr>
<td>STEMDENs</td>
<td>0.004</td>
<td>0.011</td>
<td>1.004</td>
<td>0.982 to 1.026</td>
</tr>
<tr>
<td>INVASIVE</td>
<td>-0.054</td>
<td>0.036</td>
<td>0.947</td>
<td>0.882 to 1.017</td>
</tr>
<tr>
<td>PER_INV</td>
<td>-3.178</td>
<td>1.568</td>
<td>0.042</td>
<td>0.002 to 0.900</td>
</tr>
</tbody>
</table>

a$\text{NATIVE}=\text{number of native stems} \geq 30.5\text{ cm within the 0.04 ha circular area round each nest.}$

$\text{MOISTURE}=\text{amount of moisture measured in soil with a RapiTest soil meter; 0 = dry, 10 = wet.}$

$\text{STEMDENS}=\text{density of woody vegetation} \geq 30.5\text{ cm in height} /\text{m}^2.$

$\text{INVASIVE}=\text{number of invasive species} \geq 30.5\text{ cm present within 0.04 ha circular area around each nest.}$

$\text{PER_INV}=\text{percentage of invasive stems present in the circular area around each nest.}$

RESULTS

Nest success.

Five nests were located in 2009 and 8 in 2010, for a total of 13. Mean clutch size for all nests was 3.85 (SE = 0.15). Apparent success, which is the proportion of observed nests that are successful, was 69%. Three of the 4 failed nests were lost to predation.

The goodness-of-fit test indicated the global model fit the observed values ($\chi^2 = 6.61, P = 0.581$). The highest ranking model was the percentage of invasive stems present in the plot (PER_INV; AICc = 15.978, $w_i = 0.616$; Table 1). The next best model was PER_INV + MOISTURE ($\Delta_i = 2.884, w_i = 0.146$; Table 1). We also evaluated the importance of each covariate individually (Burnham and Anderson 2002). Odds ratios are considered meaningful when 95% confidence intervals do not overlap zero. The odds ratios suggested that nesting success decreased with an increase in percentage of invasive woody vegetation. Additionally, for every native stem in the plot, the probability of success increased by 1.02 (Table 2).

Across all nest sites, the percentage of invasive woody stems in the plot averaged 38.1% (SE = 6.94). At successful nest sites, the percentage of invasive woody stems (30.3% ± 8.64; $X \pm SE$) was significantly less than at unsuccessful nest sites (55.8% ± 5.41; $t_1 = 6.74, P = 0.021$). Stems of native species did not vary between successful and failed nests ($t_1 = 0.034, P = 1.0$; Fig. 2). Multiflora rose, tatarian honeysuckle, and autumn olive were the dominant invasives; they occurred at 85%, 77%, and 51% of our plots, respectively, and accounted for 9.9%, 10.9%, and 3.3% of the total stem count. Total stem density varied greatly across nest sites (84.23 ± 16.33; range = 12.0 – 195.0). Soil moisture was rated as dry to slightly moist across nest sites (2.15 ± 0.29).

Habitat selection.

A Hosmer and Lemeshow (2000) goodness-of-fit test indicated that the global model fit the observed values ($\chi^2 = 5.01$,}
P = 0.661). The highest ranking model described the effect of percent of invasive stems on nest site selection (PER_INV) and was the only one considered substantially supported (AICc = 34.770, \( wi = 0.492 \); Table 3). We also evaluated the importance of each covariate individually (Burnham and Anderson 2002). Odds ratios indicated that habitat used by woodcock for nesting decreased with an increase in percentage of invasive vegetation present (Table 4).

Invasive vegetation comprised 57.1% (SE = 5.86) of the woody vegetation on random plots. Mean soil moisture (2.09 ± 0.21) and stem density (81.2 ± 10.24) did not vary between used and random locations. Total woody vegetation stems ≥ 30.5 cm in height per plot did not vary (\( \chi^2_{24} = 0.29, P = 0.772 \)) across nest sites (84.23 ± 16.33) and random sites (78.09 ± 12.98). We did, however, detect a significantly lower percentage of invasive vegetation between nest sites and random sites (\( \chi^2_{24} = 2.04, P = 0.050 \)). Native stem density was not different on nest sites and random sites (\( \chi^2_{24} = 1.41, P = 0.174 \); Fig. 3). Multiflora rose and tatarian honeysuckle were present on 100% of the random sites compared to 85% and 77% of nest sites, respectively (Table 5). Additionally, multiflora rose and tatarian honeysuckle comprised 50% of the total stem count on random sites compared to 95% (\( \chi^2_{24} = 9.01, P = 0.003 \); Fig. 4).

**Table 3.** Model selection results, bias-corrected Akaike's Information Criterion (AICc), model weights (\( wi \)), and parameters estimated (\( K \)) used to evaluate nest site habitat selection of American woodcock in Swatara State Park, Schuylkill & Lebanon Counties, PA, USA during 2009–2010.

<table>
<thead>
<tr>
<th>Model*</th>
<th>AICc</th>
<th>( \Delta_i )</th>
<th>( wi )</th>
<th>( K )</th>
</tr>
</thead>
<tbody>
<tr>
<td>PER_INV</td>
<td>34.770</td>
<td>0.000</td>
<td>0.492</td>
<td>3</td>
</tr>
<tr>
<td>INVASIVE</td>
<td>36.926</td>
<td>2.156</td>
<td>0.167</td>
<td>2</td>
</tr>
<tr>
<td>PER_INV + MOISTURE</td>
<td>37.301</td>
<td>2.531</td>
<td>0.139</td>
<td>2</td>
</tr>
<tr>
<td>NATIVE</td>
<td>38.516</td>
<td>3.746</td>
<td>0.076</td>
<td>3</td>
</tr>
<tr>
<td>INVASIVE + MOISTURE</td>
<td>39.440</td>
<td>4.670</td>
<td>0.097</td>
<td>3</td>
</tr>
<tr>
<td>STEMdens</td>
<td>40.472</td>
<td>5.702</td>
<td>0.046</td>
<td>2</td>
</tr>
<tr>
<td>MOISTURE</td>
<td>40.492</td>
<td>5.722</td>
<td>0.028</td>
<td>2</td>
</tr>
<tr>
<td>GLOBAL</td>
<td>40.896</td>
<td>6.126</td>
<td>0.023</td>
<td>3</td>
</tr>
<tr>
<td>NATIVE + MOISTURE</td>
<td>41.003</td>
<td>6.234</td>
<td>0.022</td>
<td>3</td>
</tr>
</tbody>
</table>

*PER_INV = percentage of invasive stems present in 0.04 ha circular area around each nest.
INVASIVE = number of invasive species ≥ 30.5 cm present within 0.04 ha circular area around each nest.
MOISTURE = amount of moisture measured in soil with a RapiTest soil meter; 0 = dry, 10 = wet.
NATIVE = number of native stems ≥ 30.5 cm within 0.04 ha circular area around each nest.
STEMdens = density of woody vegetation ≥ 30.5 cm in height /m².
GLOBAL = contains all measured variables.

**Figure 2.** Observed mean values (±1 SE) for invasive and native woody vegetation recorded at American woodcock nest sites in Swatara State Park, Schuylkill & Lebanon Counties, PA, USA during 2009–2010.

**Figure 3.** Observed mean values (±1 SE) for invasive and native woody vegetation recorded at American woodcock nest and randomly selected sites in Swatara State Park, Schuylkill & Lebanon Counties, PA, USA during 2009–2010.

**Table 4.** Akaike-weighted odds ratios of variables occurring in models of nest site habitat selection in Swatara State Park, Schuylkill & Lebanon Counties, PA, USA during 2009–2010.

<table>
<thead>
<tr>
<th>Variablea</th>
<th>( \beta )</th>
<th>SE</th>
<th>Odds Ratio</th>
<th>95% Confidence Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>NATIVE</td>
<td>0.014</td>
<td>0.011</td>
<td>1.010</td>
<td>0.993 – 1.037</td>
</tr>
<tr>
<td>MOISTURE</td>
<td>0.102</td>
<td>0.375</td>
<td>1.107</td>
<td>1.051 – 2.310</td>
</tr>
<tr>
<td>STEMdens</td>
<td>0.002</td>
<td>0.008</td>
<td>1.002</td>
<td>0.982 – 1.018</td>
</tr>
<tr>
<td>INVASIVE</td>
<td>−0.035</td>
<td>0.021</td>
<td>0.965</td>
<td>0.882 – 1.006</td>
</tr>
<tr>
<td>PER_INV</td>
<td>−2.015</td>
<td>0.891</td>
<td>0.133</td>
<td>0.002 – 0.765</td>
</tr>
</tbody>
</table>

aNATIVE = number of native stems ≥ 30.5 cm present within 0.04 ha circular area around each nest.
MOISTURE = amount of moisture measured in soil with a RapiTest soil meter; 0 = dry, 10 = wet.
STEMdens = density of woody vegetation ≥ 30.5 cm in height /m².
INVASIVE = number of invasive species ≥ 30.5 cm present within 0.04 ha circular area around each nest.
PER_INV = percentage of invasive stems present in 0.04 ha circular area around each nest.
20% on nest sites (Table 5). Occurrence of autumn olive was also higher at random sites than at nesting sites (Table 5). White ash was the most prevalent native species and was found consistently on both nest and random points; however, it only comprised a low percentage of the total stem density. Southern arrowwood (Viburnum dentatum), northern spicebush (Lindera benzoin), greenbrier (Smilax rotundifolia), and blackhaw viburnum (Viburnum prunifolium) accounted for the highest percentage of the total stem count (Table 3).

### DISCUSSION

The number of nests we located over the course of this study was comparable to previous studies (Parris 1986, Chambers 1976, Bourgeois 1977, Kinsley and Storm 1988, Harris et al. 2009). We found our apparent nest success rate of 69% to be consistent with the range of rates (50–85%) reported by previous research (Mendall and Aldous 1943, Liscinsky 1972, Gregg 1984). Nest success was greater in plots containing a lower percentage of invasive stems and models that included the percentage of invasive woody vegetation within the nest plot ranked highest in our nest success model set. Models that included the percentage of invasive woody vegetation within the plot also ranked high in our habitat selection model set. Nesting habitat selection appeared to be strongly associated with an avoidance of invasive shrubs, particularly multiflora rose and tatarian honeysuckle and we suggest that the factors involved in this avoidance are deserving of further investigation. Soil moisture and stem density did not appear to influence habitat selection however woodcock typically nest on drier sites (Liscinsky 1972, Gregg and Hale 1977, Coon et al. 1982) and we did experience dry weather during the course of the study.

Woodcock are cryptically colored and well adapted to nest on the ground, and their eggs are mottled and blend in with the leaf litter. They are well adapted to visually detect predators while nesting as evidenced by the location of the eyes towards the back of the head allowing woodcock to see in nearly a 360° arc (Mendall and Aldous 1943). Moreover, the low stem density in our study indicated that woodcock appeared to nest in less-dense cover. Tirpak et al. (2006) suggested that ruffed grouse (Bonasa umbellus), which also nest on the ground, may not rely on dense understory vegetation to avoid predators due to well-camouflaged plumage. Conversely, invasive woody vegetation can form a dense understory and rapidly degrade native habitat (Underwood et al. 1996, Deering and Vankat 1999, Kaufman and Kaufman 2007). Multiflora rose can form nearly impenetrable thickets which exclude native vegetation (Kaufman and Kaufman 2007), and bush honeysuckles may exhibit allelopathic effects, preventing other shrubs from going in close proximity to it (Williams 1994). Additionally, Rhoads and Block (2000) reported that multiflora rose and tatarian honeysuckle leaf out much earlier than native shrubs in Pennsylvania. If woodcock nesting locations are chosen in areas that are composed of a high percentage of invasive shrubs, the early leaf out and dense growth may prohibit detection of approaching predators. However we do acknowledge that the low number of nests makes our results preliminary. In support of our findings, Borgmann and Rodewald (2004)
reported that nest success was lower for American robin (Turdus migratorius) nests located in invasive shrubs and invasive shrubs reduced the nesting success of forest birds.

Previous studies of woodcock habitat preference do not include much information on invasive woody vegetation, most likely because invasives were not as widespread at the time of the studies. Current woodcock habitat management, however, must address exotic invasive woody vegetation effects and we are the first to document this relationship. We believe this is vital if the national objective of returning American woodcock populations to 1970s levels (Kelley and Williamson 2008) is to be successful.

Throughout woodcock range, habitat loss and degradation are a major cause of population decline and creating and maintaining young forested habitat is important to returning woodcock populations to past levels. Such efforts will be difficult where invasive vegetation is present. Treating invasive vegetation is expensive and managers should utilize tools that are most cost-effective. The odds of native woody vegetation competing with or out-competing invasive woody vegetation can greatly increase with proper invasive control methods like prescribed fire. Timing of control methods is critical to effectively combating invasive vegetation (Richburg 2005). By conducting repeated growing season fire treatments, which reduce the plant’s vigor, further stress can be placed on the root system. This stress decreases sprout vigor, causes root death, and increases the vulnerability of the plant to competition and disease (Richburg 2005). Because exotic invasive vegetation is extremely resilient, exotic invasive shrub control should occur over long periods of time and will require a tremendous amount of work and effort from biologists, land managers, and the public. The continued conservation of American woodcock and their habitats, however, greatly outweighs the costs of such efforts.

ACKNOWLEDGMENTS

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