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## Observer Bias and the Detection of Low-Density Populations

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1 Running head: Observer bias and surveying invasive species

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3 Observer bias and the detection of low-density populations

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24 **Abstract**

25 Monitoring programs increasingly are used to document the spread of invasive species in the  
26 hope of detecting and eradicating low-density infestations before they become established.  
27 However, interobserver variation in the detection and correct identification of low-density  
28 populations of invasive species remains largely unexplored. In this study, we compare the  
29 abilities of volunteer and experienced individuals to detect low-density populations of an actively  
30 spreading invasive species and we explore how interobserver variation can bias estimates of the  
31 proportion of sites infested derived from occupancy models that allow for both false negative  
32 *and* false positive (misclassification) errors. We found that experienced individuals detected  
33 small infestations at sites where volunteers failed to find infestations. However, occupancy  
34 models erroneously suggested that experienced observers had a higher probability of falsely  
35 detecting the species as present than did volunteers. This unexpected finding is an artifact of the  
36 modeling framework and results from a failure of volunteers to detect low-density infestations  
37 rather than from false positive errors by experienced observers. Our findings reveal a potential  
38 issue with site occupancy models that can arise when volunteer and experienced observers are  
39 used together in surveys.

40

41 Keywords: Citizen science, hemlock woolly adelgid, invasive species, monitoring, occurrence  
42 probability, site occupancy models, survey, volunteer

43

44 **Introduction**

45 The growing threat posed by invasive species has focused increased attention on the  
46 importance of documenting the distribution and spread of introduced organisms. Monitoring

47 programs aimed at detecting low-density 'founder' populations can play a critical role in slowing  
48 or even stopping the spread of harmful invasives by identifying recently-established populations  
49 that can be targeted for control and/or eradication (Lodge et al. 2006). Even partially successful  
50 programs of this sort can lower densities sufficiently for Allee effects and stochastic events to  
51 substantially increase the probability of subsequent population collapse (Liebhold and Tobin  
52 2008). These efforts have proven remarkably successful against actively-dispersing species like  
53 the gypsy moth, *Lymantria dispar* L., that respond to pheromones or other cues (e.g., the gypsy  
54 moth 'Slow the Spread' program; Sharov et al. 2002). Low-density populations of species that  
55 disperse passively by means of wind, water, or phoresy, however, often prove far more difficult  
56 to locate. Without the ability to attract the organisms to a trapping location, researchers face the  
57 often-daunting task of repeatedly searching potential habitats for low-density populations of the  
58 invading species.

59         The challenges of successfully completing the labor-intensive surveys necessary to  
60 document the spread of invasive species have been met in part by volunteer-based or 'citizen  
61 science' monitoring programs (e.g., CitSci.org). Such programs rely on concerned individuals,  
62 from schoolchildren to retirees, as cost-effective early warning and continual monitoring systems  
63 that provide the primary data for large-scale scientific studies and management responses. There  
64 are now more than 200 citizen-science programs operating in North America and their popularity  
65 is growing worldwide (Cohn 2008).

66         Although the educational and scientific benefits of volunteer-based invasive species  
67 monitoring programs are clear, the reliability of data collected by novice individuals has  
68 sometimes been questioned (Cohn 2008, Delaney et al. 2008). These concerns stem mostly from  
69 a lack of studies comparing the quality of volunteer- versus professionally-collected data rather

70 than from studies demonstrating that volunteers collect unreliable data. In the context of  
71 monitoring low-density populations of invasive species, the main concern is that novice  
72 observers may have a lower probability of detecting the species when it present and/or a higher  
73 probability of misidentification (i.e., falsely observing the species as present when it is in fact  
74 absent) than do experienced individuals. If true, then differences in the ability of observers to  
75 detect and correctly identify low-density populations of invasive species may represent an  
76 important, but largely undocumented source of sampling variation and bias in invasive species  
77 monitoring programs.

78         The detectability of species and observer bias both have important implications for  
79 documenting current distributions of invasive species and for developing reliable estimates of  
80 changes in these distributions. Site occupancy modeling (MacKenzie et al. 2006) has emerged in  
81 recent years as a means of estimating the proportion of sites truly occupied by a species given  
82 that organisms are often detected imperfectly, i.e., the probability of detecting the species is often  
83 less than one. If the probability of detecting a species is  $<1$ , as is certainly the case for low-  
84 density populations of actively spreading invasive species, then some individuals will go  
85 undetected and the actual number of occupied sites will be greater than the number of sites at  
86 which the species was actually detected. The initial model developed for estimating site  
87 occupancy rates (MacKenzie et al. 2002) considered only the possibility of 'false negatives',  
88 cases in which the species is present at a location but goes undetected. Royle and Link (2006)  
89 extended the MacKenzie et al. (2002) model to include the possibility of 'false positives',  
90 situations in which observers misidentify the target species and report it as present when the  
91 species is in fact absent. If misidentifications are common in a survey, then the true number of  
92 sites occupied could be less than the number of sites at which the species was observed. Even

93 low false positive rates have been shown to induce extreme bias in estimates of the proportion of  
94 occupied sites (Royle and Link 2006), but the impacts of observer bias on estimates of the  
95 proportion of sites infested by invasive species remains poorly explored.

96 In this study, we first compare the abilities of inexperienced volunteers and experienced  
97 observers to detect low-density populations of an actively spreading forest pest, the hemlock  
98 woolly adelgid. We then use these data to explore the general question of how interobserver  
99 variation can bias estimates of the proportion of sites infested derived from occupancy models.  
100 We hypothesized that relative to experienced observers, novice individuals should be less likely  
101 to detect low-density populations and would be more prone to misidentification of the study  
102 species. To explore these hypotheses, we use maximum likelihood methods to select among  
103 occupancy models that consider differences in the ability of observers to both detect and  
104 correctly identify the hemlock woolly adelgid. We parameterize these models using data from a  
105 420-tree survey conducted by nine volunteers and three experienced individuals. Our results  
106 support the notion that volunteers and experienced observers differ in their ability to detect low-  
107 density populations and that such differences in observer ability can bias estimates of the  
108 proportion of sites occupied. However, this bias manifests itself in unexpected ways.

109

## 110 **Materials and Methods**

### 111 *Study species*

112 The hemlock woolly adelgid, *Adelges tsugae* Annand ('HWA'; Hemiptera: Adelgidae) is  
113 an actively-spreading invasive pest of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and  
114 Carolina hemlock (*Tsuga caroliniana* Englemann) in the eastern United States (McClure and  
115 Cheah 1999). HWA is a minuscule (<1-mm long adult), flightless insect that in the US is both

116 obligately parthenogenetic and exclusively passively dispersed (McClure 1990). The  
117 parthenogenetic nature of HWA means that even a single colonizing individual can start a new  
118 infestation, producing an initially low-density population that only can be detected by costly and  
119 time-consuming surveys (Evans and Gregoire 2007). Further, Costa and Onken (2007) list  
120 several objects common on hemlock foliage that might be confused with HWA by observers  
121 with varying skill levels. These include spider ovisacs, pine sap from adjacent conifers, froth  
122 from spittle bugs, and wool from white pine aphids blown from neighboring trees.

123

#### 124 *Study area*

125         We sampled hemlock trees in the 487-ha Cadwell Memorial Forest in Pelham,  
126 Massachusetts (N42.37°, W72.42°), an experimental forest managed by the University of  
127 Massachusetts at Amherst. Cadwell Forest is located in the central hardwood region of southern  
128 New England and includes discrete stands of eastern hemlock. Before 2007, no HWA  
129 infestations had been detected at Cadwell Forest and the local hemlock trees appeared uniformly  
130 healthy (J. Elkinton, unpublished data). In the late winter of 2008, however, ad hoc surveys  
131 revealed low levels of HWA infestations on several trees. Hemlock stands in this forest thus  
132 provide an ideal venue to compare the ability of volunteer and experienced observers to detect  
133 early low-density HWA invasions.

134

#### 135 *Sampling design*

136         Hemlock often grows in nearly monospecific stands that are patchily distributed across  
137 the landscape (Ellison et al. 2005). We selected five hemlock stands ( $\sim 1 \times 10^4$  m<sup>2</sup> each) for  
138 sampling that were primarily (>50%) comprised of hemlock trees  $\leq 10$  m in height such that a

139 portion of each tree could be sampled from the ground. All stands were bordered by hardwood  
140 forests, allowing the natural boundaries of each stand to be readily identified. Within each stand,  
141 all hemlock trees  $\geq 0.5$  m in height were numbered using aluminum tags and marked with  
142 flagging tape to improve visibility. We marked a total of 420 hemlock trees in the five stands  
143 (mean number of trees per stand = 80, range = 31 to 146).

144 Twelve observers participated in the sampling effort: three experienced individuals who  
145 perform field research on HWA and nine volunteers who had no prior experience sampling for  
146 HWA. Prior to the sampling, the volunteers were trained for fifteen minutes on the sampling  
147 methodology (see below) and on identifying HWA infestations, including objects that could be  
148 confused with HWA. Each person was then assigned to one of four groups (n=3 persons per  
149 group). Two of the groups entirely were comprised of volunteers (hereafter referred to as  
150 'volunteer-only'). The remaining two groups contained one experienced and two volunteer  
151 individuals and two experienced and one volunteer individual (hereafter referred to as  
152 'volunteer/experienced'). Each group was provided a numbered list of trees to sample that could  
153 be located in the field by the corresponding numbered tag on each tree. To control for possible  
154 heterogeneity in infestation and detection rates between stands, each group was randomly  
155 assigned trees to sample in multiple stands.

156 Our sampling design followed the protocol described by MacKenzie et al. (2006) for a  
157 single-species, single-season occupancy model, with individual hemlock trees regarded as sites.  
158 Occupancy modeling requires that sites must be visited by at least two independent observers,  
159 with each observer recording the presence/absence of the target species at each site. In this study,  
160 three observers from the same group visited each tree independently. Observers searched all  
161 accessible branches for evidence of white woolly masses characteristic of the HWA sistens



162 generation. Each search continued until either HWA was detected or a two-minute sampling  
163 period had expired. To ensure that sampling was independent, no two observers sampled a tree at  
164 the same time and observers were instructed not to communicate the infestation status of trees to  
165 the other observers in their group. Sampling occurred on April 26<sup>th</sup>, 2008, when the white woolly  
166 masses produced by HWA are at their largest and most visible; this time period is generally  
167 considered the optimal sampling period for HWA (Costa and Onken 2007). The sessile nature of  
168 the HWA sistens generation precludes any changes in infestation status during our study.

169         To examine whether there were differences between volunteers and experienced  
170 individuals in terms of the density of infestations detected by each type of observer, two  
171 experienced individuals involved in the original survey returned the following week to all trees  
172 where HWA was detected. All accessible branches thoroughly were searched and the number of  
173 white woolly masses observed on the tree was counted. This second, more thorough survey  
174 provided an estimate of the number of detectable individuals on the tree. We used a paired t-test  
175 on log-transformed HWA abundance to compare the mean abundance of HWA infestations that  
176 were detected by any of the nine volunteers to the mean abundance of HWA infestations that  
177 were detected by only the three experienced individuals and but not by any of the nine  
178 volunteers.

179

### 180 *Occupancy modeling*

181         We examined how differences in detection abilities between observers influence  
182 estimates of the proportion of infested hemlock trees. The occupancy model framework proposed  
183 by Royle and Link (2006) allows the estimation of three parameters:  $\psi$ , the proportion of sites  
184 occupied (in our case, the proportion of infested hemlock trees), and two classification

185 probabilities. These probabilities are (A)  $p_{11}$ , the 'detection probability', the probability of  
 186 detecting the species, given that the species is actually present at the site; and (B)  $p_{10}$ , the  
 187 'misclassification probability', the probability of falsely detecting the species at an unoccupied  
 188 site. Given our randomized sampling design, the number of trees sampled by each observer  
 189 (minimum  $n=85$ , Tables 1 & 2), and the sessile nature of HWA, heterogeneity in detection and  
 190 misclassification probabilities should result almost entirely from interobserver variation.

191 We considered four models that make different assumptions regarding  $p_{11}$  and  $p_{10}$ . The  
 192 simplest model was the standard framework proposed by MacKenzie et al. (2002) that assumes  
 193 false positives are not possible ( $p_{10} = 0$ ) and that detection probabilities are constant across  
 194 observers, or " $\psi; p_{11}(\cdot); p_{10}(0)$ ". The second model again assumes that false positives were not  
 195 possible, but allows observers to differ in their probability of detecting HWA: " $\psi; p_{11}(t); p_{10}(0)$ ".  
 196 The final two models both incorporate the possibility of misclassification ( $p_{10} > 0$ , Royle and  
 197 Link 2006), with the simpler of the two assuming that observers do not differ in their probability  
 198 of detecting or misclassifying HWA: " $\psi; p_{11}(\cdot); p_{10}(\cdot)$ ". The more complex of these two models  
 199 assumes that observers can differ in their probability of detecting and misclassifying HWA:  
 200 " $\psi; p_{11}(t); p_{10}(t)$ ". Maximum-likelihood estimates of the model parameters can be obtained by  
 201 maximizing numerically

$$202 \quad L(p_{11}, p_{10}, \psi \mid y) \propto \prod_{i=1}^n \left\{ p_{11}^{y_i} (1 - p_{11})^{T - y_i} \right\} \psi + \left[ p_{10}^{y_i} (1 - p_{10})^{T - y_i} \right] (1 - \psi),$$

203 where  $n$  is the number of sites (trees),  $T$  is the number of samples (observers), and  $\mathbf{y} = \{ y_{i=1}^n \}$   
 204 with  $y_i$  representing the site-specific number of detections. See Royle and Link (2006) for  
 205 details. We used the small sample size form of Akaike's Information Criterion ( $AIC_c$ ) to  
 206 determine the model best supported by the data (Burnham and Anderson 2002). Statistical

207 analyses were performed in R 2.7.2 (R Development Core Team 2006) using code modified from  
208 Royle and Link (2006) and in Microsoft Excel using Excel spreadsheets developed by Donovan  
209 and Hines (2007). Sample data, R code, and Excel spreadsheets are provided in the Supplement  
210 to this paper.

211

## 212 **Results**

213         The two volunteer-only groups detected HWA infestations on a smaller proportion of  
214 trees than did the two volunteer/experienced groups. One of the volunteer-only groups detected  
215 HWA on 14 of 86 sampled trees (naïve infestation rate = 0.163), and the other on 33 of 95 trees  
216 (naïve infestation rate = 0.347). In contrast, the two volunteer/experienced groups detected HWA  
217 on 57 of 125 trees (naïve infestation rate = 0.456) and on 69 of 114 trees (naïve infestation rate =  
218 0.605). Of the two volunteer/experienced groups, the group with the fewest volunteers realized  
219 the highest overall naïve infestation rate (0.605). When two experienced observers returned to  
220 the 173 trees to estimate the abundance of detected HWA infestations, HWA was found on 164  
221 trees. Experienced individuals detected smaller HWA infestations than volunteers (paired t-test,  
222  $p = 0.017$ ).

223         The form of the best-supported model differed between volunteer-only groups and  
224 volunteer/experienced groups. For volunteer-only groups, model comparison by  $\Delta AICc$  and  
225 normalized Akaike model selection weights (Burnham and Anderson 2002) revealed that models  
226 where the probability of misidentifying HWA was zero ( $p_{10} = 0$ ) were best supported by the data  
227 (Table 1). However, the best-supported model for volunteer-only groups differed in their  
228 assumptions regarding whether observers differed in their probability of detecting HWA  
229 infestations. The best-supported model for one of the volunteer-only groups assumed that

230 observers differed in their detection probabilities,  $\psi p_{11}(t)p_{10}(0)$ , while the data for the other  
231 volunteer-only group most strongly supported the model  $\psi p_{11}(\cdot)p_{10}(0)$ , which did not make this  
232 assumption. In contrast, the form of the best-supported model was the same for both  
233 volunteer/experienced groups (Table 2). For such groups, strongest support was for model  
234  $\psi p_{11}(t)p_{10}(t)$ , where misclassification probabilities were greater than zero and both detection and  
235 misclassification probabilities differed between observers. There was little support for models  
236 where experienced and volunteer observers were assumed to have equal probabilities of  
237 detecting HWA infestations.

238         When compared to volunteers in their group, experienced observers had a higher  
239 probability of detecting HWA infestations (Table 2). Unexpectedly, this was also true of the  
240 probability of misclassifying other organisms as HWA, with experienced observers having a  
241 higher probability of misclassifying HWA infestations than volunteers. This finding is an artifact  
242 of the models, the origin of which we discuss below. When comparing across groups, estimates  
243 of detection probabilities from the best-supported models ranged from 0.28-0.94, with the  
244 highest value obtained by an experienced observer and the lowest by a volunteer (Tables 1, 2).  
245 Detection probabilities for experienced observers were always greater than 0.75 and had a  
246 smaller range than those of volunteers (0.19 versus 0.44).

247         Estimates of the proportion of trees infested from the best-supported models ranged from  
248 0.12-0.41. For volunteer-only groups, the estimated infestation rate was higher than the naïve  
249 infestation rate (Table 1). In contrast, the estimated infestation rate was considerably lower than  
250 the naïve infestation rate for groups containing an experienced observer (Table 2).

251

252 **Discussion**

253           The reliability of data collected from field surveys is directly related to sampling  
254 variation and bias in the methods used to gather the data and interobserver variation is one such  
255 source of bias. Our findings suggest that observer experience can be an important source of  
256 sampling variation and bias in the detection of low-density populations. However, when such  
257 surveys are used in an occupancy modeling framework that allows for misidentification,  
258 interobserver bias can be manifested in an unexpected manner.

259           We found that experienced observers differed from volunteers in their ability to detect  
260 low-density infestations. Relative to volunteers, experienced observers (1) detected infestations  
261 at a greater proportion of trees, (2) had a higher probability of detecting infestations, and (3)  
262 detected smaller infestations. Although we were not surprised by these findings, we were  
263 surprised by the apparent result that experienced observers were *more* likely to misclassify HWA  
264 than volunteers. Although the possibility that experienced individuals are more likely to  
265 misidentify HWA cannot be discounted, Costa and Onken (2007) note that once detected, HWA  
266 are nearly unmistakable to a well-trained individual. An alternative explanation is suggested by a  
267 closer inspection of the detection histories (Table 3). For the team with one experienced observer  
268 and two volunteers, the two volunteer observers detected HWA on only 1 of 125 trees when the  
269 experienced observer did not. In contrast, the experienced individual detected HWA 23 times  
270 when the two volunteers did not. However, when the infested trees were resurveyed by two  
271 experienced observers to estimate the abundance of HWA, this additional survey detected  
272 infestations on 19 of these 23 trees. The detection histories for the group with two experienced  
273 individuals reveal a similar pattern.

274           Taken together, our results (A) suggest a failure by volunteers to detect low-density  
275 infestations rather than misidentification by experienced observers and (B) reveal an issue  
276 regarding the absence of statistical weighting in the model. In essence, the misclassification  
277 model assumes that there are two types of sites and the probability of detection is lower at one  
278 type of site than the other. The differences in detection probabilities between these two sites can  
279 arise either through misclassification (Royle and Link 2006) or through heterogeneity in  
280 detection. In this study, heterogeneity in detection associated with variation in abundance of  
281 HWA and differences in the ability of observers to detect low-density populations, rather than  
282 misclassification, is the factor most likely to be driving differences in detection between sites. In  
283 other words, the two types of sites in our study are those with relatively dense infestations that  
284 were detected by both volunteers and experienced observers and those with relatively low  
285 density infestations that were detected only by experienced individuals. However, as formulated,  
286 our models give equal weight to the quality of any individual's observations. Therefore, when a  
287 low-density infestation is detected by one experienced observer, but missed by the remaining two  
288 volunteers, statistical support tips in favor of misclassification. This issue became apparent only  
289 when surveys completed by experienced observers were paired with those made by volunteers.  
290 Thus our findings caution against the use of observers of differing levels of experience in the  
291 same survey and suggest the need to include in models that allow for false positive errors survey-  
292 specific covariates that account for biases in detection probabilities introduced by differences in  
293 observers (e.g., Bailey et al. 2004).

294           Our findings also speak to how strongly misidentifications can bias estimates of the  
295 proportion of sites occupied (Royle and Link 2006). In the most extreme case, the modeled  
296 proportion of infested trees was nearly 4 times lower (0.12 versus 0.58, naïve infestation =

297 0.456), when misclassification probabilities were assumed to be greater than zero versus when  
298 they were assumed to be zero. Again, the modeled rate of 0.12 when misclassification  
299 probabilities were assumed to be greater than zero appears to be primarily a function of the  
300 model's spurious interpretation of valid detections made by experienced observers as instances of  
301 misclassification.

302         What do our results say about the adequacy of data on the distribution of low-density  
303 populations collected by volunteers? We suggest that the answer to this question depends on the  
304 ultimate use of the data and on the system under study. For example, recent studies have  
305 demonstrated that volunteers can provide accurate data on the presence of invading species  
306 (Boudreau and Yan 2004; Delaney et al. 2008). These studies, both involving aquatic invasive  
307 species, dealt with either a relatively large and easy-to-detect organism (Delaney et al. 2008) or  
308 used volunteers to collect samples that were later verified by professionals (Boudreau and Yan  
309 2004). In contrast, HWA, though easy to identify to the trained eye, can be extremely difficult to  
310 detect when occurring at low densities (Evans and Gregoire 2007); our results suggest field  
311 experience can improve the ability to detect such infestations. Thus, we argue our findings speak  
312 more to issues regarding the importance of properly training volunteers and to the challenges of  
313 monitoring low-density or difficult-to-detect organisms (e.g., Milberg et al. 2008), rather than to  
314 the reliability of volunteer-based monitoring programs per se. For example, Lotz and Allen  
315 (2007) found that there was no difference in error rates between professional scientists and  
316 volunteers who had received the same training and who had little difference in actual field  
317 anuran-call-survey experience (see also Shirose et al. 1997; Genet and Sargent 2003). Further,  
318 multiple studies have demonstrated that observer bias generally decreases as observers become  
319 more experienced (Sauer et al. 1994; McLaren and Cadman 1999; Delaney et al. 2008). Taken

320 together, our results underscore the importance of adequate training for volunteers taking part in  
321 monitoring programs and the need to document and account for interobserver variation in  
322 analytical estimates of site occupancy rates (Lotz and Allen 2007; Pierce and Gutzwiller 2007).  
323 Future work in this area should consider the role of survey-specific covariates that account for  
324 interobserver variation in detection probabilities.

325

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331

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385 Table 1 – Comparison of models and parameter estimates for detection of HWA for groups  
 386 comprised entirely of volunteers. K, number of parameters in model;  $\Delta\text{AICc}$ , small sample size  
 387 form of Akaike’s information criterion (AICc) for each model, minus the AICc of the model with  
 388 minimum AICc;  $w$ , normalized model selection weights;  $p_{11}$ , the probability of detecting the  
 389 species given that the species is actually present at the site;  $p_{10}$ , the probability of falsely  
 390 detecting the species at an unoccupied site. For model notation, symbols within parentheses  
 391 indicate whether probabilities are assumed to be constant (·) or different (t) across surveys.

	$\Delta\text{AICc}$	$w$	K	$\psi$ -hat	$p_{11,1}$	$p_{11,2}$	$p_{11,3}$	$p_{10,1}$	$p_{10,2}$	$p_{10,3}$
$n = 95, \psi_{\text{naïve}} = 0.347$										
$\psi; p_{11}(t); p_{10}=0$	0	0.85	4	0.41	0.28	0.43	0.61	0	0	0
$\psi; p_{11}(\cdot); p_{10}=0$	4.47	0.09	2	0.43	0.43	0.43	0.43	0	0	0
$\psi; p_{11}(t); p_{10}(t)$	6.57	0.03	7	0.39	0.27	0.46	0.65	0.02	0.00	0.00
$\psi; p_{11}(\cdot); p_{10}(\cdot)$	6.61	0.03	3	0.43	0.43	0.43	0.43	0.00	0.00	0.00
$n = 86, \psi_{\text{naïve}} = 0.163$										
$\psi; p_{11}(\cdot); p_{10}=0$	0	0.62	2	0.17	0.72	0.72	0.72	0	0	0
$\psi; p_{11}(\cdot); p_{10}(\cdot)$	1.68	0.27	3	0.15	0.78	0.78	0.78	0.01	0.01	0.01
$\psi; p_{11}(t); p_{10}=0$	3.44	0.11	4	0.17	0.63	0.77	0.77	0	0	0
$\psi; p_{11}(t); p_{10}(t)$	9.34	0.01	7	0.14	0.67	0.86	0.86	0.01	0.01	0.01

392

393 Table 2 – Comparison of models and parameter estimates for detection of HWA for groups  
 394 comprised of both volunteers (V) and experienced observers (E, parameter estimates for  
 395 experienced individuals are italicized). K, number of parameters in model;  $\Delta AICc$ , small sample  
 396 size form of Akaike’s information criterion (AICc) for each model, minus the AICc of the model  
 397 with minimum AICc;  $w$ , normalized model selection weights;  $p_{11}$ , the probability of detecting the  
 398 species given that the species is actually present at the site;  $p_{10}$ , the probability of falsely  
 399 detecting the species at an unoccupied site. For model notation, symbols within parentheses  
 400 indicate whether probabilities are assumed to be constant ( $\cdot$ ) or different (t) across surveys.

	$\Delta AICc$	$w$	K	$\psi$ -hat	$p_{11,1}$	$p_{11,2}$	$p_{11,3}$	$p_{10,1}$	$p_{10,2}$	$p_{10,3}$
n = 114, $\psi_{naïve} = 0.605$					E	E	V	E	E	V
$\psi; p_{11}(t); p_{10}(t)$	0	0.65	7	0.26	<i>0.78</i>	<i>0.75</i>	0.34	<i>0.07</i>	<i>0.44</i>	0.01
$\psi; p_{11}(t); p_{10}=0$	1.2	0.35	4	0.72	<i>0.36</i>	<i>0.72</i>	0.13	0	0	0
$\psi; p_{11}(\cdot); p_{10}=0$	56.71	0.00	2	0.84	<i>0.35</i>	<i>0.35</i>	0.35	0	0	0
$\psi; p_{11}(\cdot); p_{10}(\cdot)$	56.82	0.00	3	0.10	<i>0.75</i>	<i>0.75</i>	0.75	<i>0.24</i>	<i>0.24</i>	0.24
n = 125, $\psi_{naïve} = 0.456$					E	V	V	E	V	V
$\psi; p_{11}(t); p_{10}(t)$	0	0.92	7	0.12	<i>0.94</i>	<i>0.72</i>	<i>0.79</i>	<i>0.25</i>	<i>0.15</i>	<i>0.04</i>
$\psi; p_{11}(t); p_{10}=0$	5.06	0.08	4	0.58	<i>0.57</i>	<i>0.37</i>	0.22	0	0	0
$\psi; p_{11}(\cdot); p_{10}(\cdot)$	12.75	0.00	3	0.1	<i>0.84</i>	<i>0.84</i>	0.84	0.15	0.15	0.15
$\psi; p_{11}(\cdot); p_{10}=0$	19.18	0.00	2	0.61	<i>0.37</i>	<i>0.37</i>	0.37	0	0	0

401 Table 3 – Detection histories of HWA populations by group. Histories indicate whether HWA  
 402 was determined to be present (1) or absent (0) for each of the three surveys. For groups with  
 403 experienced observers surveys are ordered such that reading from left to right moves from  
 404 experienced (E) to volunteer (V) observers (e.g., 100 for the group with one experienced  
 405 observer and two volunteers indicates an instance when the experienced observer detected HWA  
 406 but the two volunteers did not).

Detection history	EEV	EVV	VVV	VVV
111	6	8	2	6
110	14	6	2	1
011	2	1	9	3
101	2	4	4	1
100	7	23	3	1
010	37	12	4	1
001	0	3	9	1
000	45	68	62	72

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