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Behavioral Indicators of Predator Space Use: Studying Species Interactions Through the Behavior of Predators

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7   **Behavioral indicators of predator space use:**

8   **Studying species interactions through the behavior of predators**

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34 **ABSTRACT**

35 Predation has major impacts on survival and reproductive success for many species. To quantify

36 these effects, ecologists often choose to intensively study prey populations to measure predation

37 rates and/or estimate predator abundance. But in some cases, predation rates are less strongly

38 related to predator abundance per se than to spatial and temporal patterns of predator space use;

39 thus quantifying the latter may provide meaningful surrogates of predation rates that scale up to

40 larger areas. This is particularly true when safety for prey, especially sessile and vulnerable

41 prey, is strongly linked to predator-free space. Our own research programs have used two

42 general types of behavioral indicators to quantify space use by predators: giving-up densities, as

43 a surrogate for patch quitting harvest rates, and activity density. We discuss two general

44 mechanisms by which predator-free (or predator-poor) space is created and link these

45 mechanisms to behavioral indicators that can be easily collected in the field. We then summarize

46 our past work on predation on passerine nests and moth pupae to demonstrate how using

47 behavioral indicators of space use can reveal much about the impact of a predator on its prey.

48 We demonstrate that behavioral indicators can be used as: (1) leading indicators for predation

49 rates, (2) surrogates for information otherwise difficult to obtain, (3) integrative measures of the

50 strength of species interactions, and may (4) reveal the outcomes of ecological interactions, such

51 as prey persistence.

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53 Keywords: behavioral indicators, foraging theory, GUDs, incidental predation, predator space

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58 **INTRODUCTION**

59 Predation has major impacts on survival and reproductive success for many species. To quantify

60 these effects, ecologists often choose to intensively study predator and prey populations to

61 measure predation rates and/or estimate predator abundance. But in some cases, predation rates

62 are less strongly related to predator abundance per se than to spatial and temporal patterns of

63 predators' space use. The consequence is that predator density can be a lagging or misleading

64 indicator of ecological relationships when the factors that govern predator space use, e.g., the

65 predator's motivational state or patch use decisions based on the local levels of risk and reward,

66 do not scale with or lag behind conspecific population density (Brown et al. 1999, Schmidt et al.

67 2001a, Pusenius and Schmidt 2002). Under these circumstances, developing informative

68 behavioral metrics (i.e., behavioral indicators) that do scale with predation rates is imperative

69 and of obvious practical value. Two metrics or behavioral indicators of predation rates we

70 consider below are quantifying the amount of space occupied by predators or the intensity at

71 which they exploit space.

72 Consider nest predation as a specific example of these points. Nest predation is often the

73 leading cause of reproductive failure in birds (Martin 1992) and other nesting organisms (e.g.,

74 turtles, Chaloupka and Limpus 1991), and thus is an important determinant of population vital

75 rates. A predator's attack on a songbird nest is the outcome of numerous behavioral decisions

76 made by the predator and prey. Perhaps none are as important as the decisions of where the

77 predator should forage and for how long. To see this, first consider that although parents can

78 actively select nest sites to reduce predation risk, nests themselves cannot move once established

79 and so prey escape tactics are relatively passive. Second, outside colonial species that rely on

80 predator satiation as a means to reduce the magnitude of predation, nests are cryptic as well as

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81   ephemeral, dispersed and occurring at low densities, and in some cases outnumbered by their

82   predators. The latter can occur because most nest predators are foraging generalists that rely on

83   a broad prey base and so can out number some classes of prey items. In New York State, for

84   instance, the 2.25-ha trapping grids managed by our colleague, Richard Ostfeld, can hold > 200

85   individual white-footed mice and eastern chipmunks in some years, whereas breeding bird

86   densities are < 10 pairs/ha and much lower when we consider only ground- or low-shrub nesting

87   species.

88   Based in part on the ratio of predator/prey abundances, the generalist feeding habitats of

89   most nest predators, and the low intake (nests often comprise $\leq$ 2% of predator diet), that many

90   predation events are incidental in nature (Vickery et al. 1992, Yanes and Saurez 1996); that is,

91   predation occurs as the result of encountering relatively rare and hence "unexpected" prey items

92   while searching for primary prey or simply occupying high quality resource patches. Hence,

93   rates of incidental predation will correlate with patterns of predator space use and exploitation,

94   and developing models or methods to track the latter will benefit from a consideration of the

95   predator's patch use behavior. We develop these explicit relationships below.

96   While we have conceptualized our ideas largely based on our empirical studies of

97   breeding songbirds (KAS) and pupae of gypsy moths (EMS), our framework should be

98   amenable to prey that are encountered largely incidentally by generalist predators, including prey

99   organisms that are relatively uncommon or ephemeral, sessile or otherwise are largely inactive

100 during at least one life history stage. For example, this can also include the vulnerable young of

101 cheetahs (Durrant 1998) and deer (Pojar and Bowden 2004). After presenting our conceptual

102 background and supporting empirical studies we expand our framework to consider incidental or

103 non-incidental prey that benefit from alternative mechanisms that 'anchor' predators in space in turn

104 creating spatial heterogeneity in predator activity that prey may find refuge in. Through developing

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105   a framework and summarizing our past work we argue that behavioral indicators of predator

106   space use can reveal much about the predator's impact on its prey and hence the habitat quality

107   and reproductive success of the prey. We will demonstrate that behavioral indicators, and the

108   framework from which they emerge, may be particularly valuable as: (1) leading as opposed to

109   lagging indicators of the magnitude of predation, (2) surrogates for information otherwise

110   difficult to obtain, (3) integrative measures of the strength of species interactions, and lastly may

111   (4) reveal novel insights into ecological interactions.

112

113   **CONCEPTUAL FRAMEWORK**

114   *Quitting harvest rates, space use, and incidental predation* – The branch of optimal foraging

115   theory known as patch-use theory has developed around the question of how much time to

116   allocate to a resource patch. The answer is generally given in the form of a patch giving-up rule.

117   In the case of prescient foragers with random search the appropriate rule is to forage until the

118   rate of resource harvest (a declining function of time spent foraging in the patch) equals the

119   accrual rate of foraging costs (Charnov 1976, Brown 1988). Brown (1988, 1994) recognized

120   three general foraging costs: predation (P), missed opportunity (MOC; the value of time should it

121   be spent on alternative fitness-enhancing activities) and metabolic (C) costs. This giving-up rule

122   is referred to as a fixed quitting harvest rate (QHR) rule because it results in patches that have

123   equal harvest rates after a forager ceases (i.e., quits) to exploit the patch irrespective of initial

124   patch quality. It can be written as: QHR = P + MOC + C. When the initial harvest rate of a

125   patch is less than P + MOC + C the patch is unprofitable (i.e., the optimal time spent foraging is

126   zero). A forager that can assess and respond to spatial heterogeneity in resource abundance

127   should exploit only those resource patches that it considers profitable (Stephens and Krebs 1986,

128   Schmidt and Brown 1996, Schmidt et al. 2001). Unprofitable and therefore unused space (i.e.,

129   predator-free space) can provide refuge that may be especially important for incidental prey;

130   prey too sparse for predators to base patch-use decisions on, yet they are attacked whenever

131   generalist predators encounter them while foraging for more common foods (Vickery et al.

132   1991).

133   The giving-up rule also indicates two general routes to patch rejection (see Fig. 1)

134   corresponding to "top-down" and "bottom-up" forces, respectively: predators reject patches

135   associated with a high risk of predation from apex predators (e.g., nest-robbing chipmunks avoid

136   patches associated with greater risk of predation from weasels) and predators reject patches

137   lacking sufficient resources (nest-robbing chipmunks avoid patches with few red maple seeds).

138   These routes are non-mutually exclusive in the sense that patch rejection always occurs because

139   there are insufficient resources to offset the high cost (including the risk of predation; Brown and

140   Kotler 2004) of foraging in the patch. Nonetheless, it is also valuable to separate these two

141   components because the abundance and distribution of resources and apex predators (maple

142   seeds and weasels, respectively, in our chipmunk example) are largely independently determined

143   (but see Sih 1998 for a summary of models that suggest apex predator abundance should match

144   the abundance of resources for its prey).

145   More formally, Schmidt et al. (2001a) constructed a model explicitly linking generalist

146   predator foraging behavior, space use, and predation rates on incidental prey. In the model,

147   predators assess patch quality and only forage in those resource patches considered profitable

148   (i.e., initial patch harvest rate exceed the predator's quitting harvest rate, QHR); unprofitable

149   space is unused (Schmidt 2004). By varying the QHR, its relationship to space use and

150   incidental predation rates could be determined (also see Schmidt et al. 2001 for explicit

151   equations). If the QHR is low (i.e., resources are extremely valuable) most patches are profitable

152   and nearly all available space is used. If the QHR is high (i.e., resources are relatively cheap or

153   predation risk is very high) many patches are unprofitable and space use declines. Therefore,

154   changing the QHR drives an inverse but non-linear change in the amount of space predators

155   forage within (Schmidt et al. 2001, Pusenius and Schmidt 2002). In one analysis of the model

156   that included uncommon incidental prey dispersed (independent of primary prey) among the

157   patches, increasing the QHR reduced incidental prey consumption. Overall consumption closely

158   mirrored predator space use when primary prey were distributed in a Poisson fashion (Fig. 3),

159   but this result may not follow for other distributions of prey or if primary and incidental prey are

160   themselves inversely correlated.

161   Space need not be treated dichotomously as predator-free or predator-occupied and this

162   fact can further strengthen the relationship between the QHR and space use. The QHR is both a

163   qualitative (predator-free/occupied) and quantitative (time spent searching for primary prey)

164   indicator of space use/exploitation. Assuming random search within a patch and holding initial

165   primary prey density fixed, search time (t) is a decreasing function of QHR or the final density of

166   primary prey remaining in a patch (Schmidt and Brown 1996). Predator-free space is equivalent

167   to patches where t=0.

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169   *Spatial anchoring and predator space use* – Within our framework of incidental predation

170   predator activity is "anchored" to high reward/low risk sites creating predator-free or predator-

171   poor space at other sites. Spatial heterogeneity in predation risk may also arise from alternative

172   mechanisms of spatial anchoring of the predator that may be important for both incidental and

173   non-incidental prey. This includes interactions with conspecifics (e.g., territoriality) and the

174 need to return to a central home location (e.g., nest or den). For example, Sergio et al. (2003)

175 observed that black kite (*Milvus migrans*) territories were aggregated within interstitial areas

176 outside the sphere of influence of its intra-guild predator, the eagle owl (*Bubo bubo*). All black

177 kite nests within 1 km of eagle owl nests were unsuccessful, and kite nests beyond 1 km showed

178 a linear increase in productivity with greater distance from owl nests. Likewise, Mech (1977)

179 noted that wolves form stable territories that are separated by buffer zones up to 2 km wide, into

180 which wolves rarely venture to avoid antagonistic interactions with neighboring packs. Nearly

181 all surviving white-tailed deer in a declining population were within these buffer zones (Taylor

182 and Perkins 1991). In this vein, Schauber (2000) modeled predator-free space as gaps between

183 individual home ranges under different assumptions of territory spacing. Uniform territory

184 spacing creates a linear decrease in predator-free space with increasing predator abundance until

185 all space is occupied, whereas random spacing results in an exponential decrease, as has been

186 observed for white-footed mice (Schmidt et al. 2006). With random territory spacing, some

187 predator-free space persists even at high predator abundance, which was critical for gypsy moth

188 persistence in Schauber's (2000) analysis. Through these mechanisms of territoriality and

189 central place foraging, predator space may not correlate well with predator abundance, leaving

190 the latter a poor indicator of predation risk to prey. Such cases call for measuring space use

191 itself.

192   We end this section by noting that colleagues have suggested to us that true predator-free

193 space does not exist – eventually predators will move through all available space. This remains

194 to be demonstrated but it does have a ring of truth; predator-free space can best be considered as

195 a transient phenomenon. But despite its transience, predator-free space can be critical when prey

196 vulnerability is short-lived. Examples include gypsy moth pupae (vulnerable for ~ 13 days) and

197 songbird nests (vulnerable for ~ 2-4 weeks) that comprise our own studies, but also includes

198   cheetahs, which are vulnerable to intraguild predation largely as young cubs, and deer, which are

199   vulnerable to predation from coyotes largely as young fawns (Pojar and Bowden 2004, Vreeland et

200   al. 2004). Survival of these prey requires their locations remain predator-free for only days or weeks

201   to have large repercussions. When prey are mobile, as when young cubs or fawns are moved, then

202   even if individual pockets of predator-free space wink on and off, the mean amount of predator-free

203   space is likely to be fairly stable in comparison.

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205   **EMPIRICAL STUDIES**

206   *Behavioral Indicators: monitoring quitting harvest rates and space use* – Quitting harvest rates

207   can be notoriously difficult to monitor in the field. Fortunately, counting the number of resource

208   items remaining within a patch after a foraging bout, known as a giving-up density or GUD,

209   often provides a useful surrogate of quitting harvest rates that is easily measured in the field

210   (Brown 1988). Food patches should yield diminishing returns such that current amount of food

211   in a patch correlates with the instantaneous harvest rate. These conditions are often easily

212   fulfilled through the use of artificial food patches (Brown 1988) created by mixing a small

213   quantity (to prevent satiation) of food (e.g., seeds) within a patch substrate (e.g., sand). Giving-

214   up densities have been widely applied to quantifying individual foraging costs (see recent review

215   by Brown and Kotler (2004), but as discussed above, GUDs collected across larger spatial scales

216   can be used as surrogates for space use (Schmidt et al. 2001).

217   The technique of giving-up densities is an important tool in the ecologist's toolbox for

218   measuring the landscape of foraging costs perceived by predators and the risk experienced by

219   prey. However, not all prey are distributed within idealized food patches that the GUD

220   technique often requires. Furthermore, the food patches themselves lure animals so that GUDs

221   do not necessarily indicate specific sites predators would not use in the absence of a baited patch.

222   There are techniques to get around some of these concerns; for example by correlating GUDs to

223   the physical landscape one may learn that a predator around foraging along habitat edges. An

224   alternative to GUDs that we discuss here is directly quantifying predator activity. Predator

225   activity density, i.e., the aggregate use of a site per unit area and time, is a more proximal

226   measure of the landscape of risk experienced by prey. Activity density reflects the total *intensity*

227   *of use* in a specific area by a number of individuals, rather than quantifying the *number* of

228   individuals. The concept of activity density is similar to the idea of population density, but

229   applies at the spatial scale of individual space use decisions. For instance, one raccoon (*Procyon*

230   *lotor*) that traverses a given patch of space 6 times in a week should represent greater risk (i.e.,

231   higher likelihood of encounter) to prey than 3 raccoons that each traverse the same patch once a

232   week. We have used two different indicators of small mammal activity density, (1) traps with

233   zero captures and (2) track plates.

234

235   *Case studies* – Schmidt and colleagues (2001, Schmidt and Ostfeld 2003) tested the explicit links

236   between QHRs (measured by GUDs), space use (quantified as the proportion single oat grains

237   removed by mice off a lattice grid arrangement) in the white-footed mouse (nest predator), and

238   predation on passerine nests (prey). They used artificial nests to increase sample sizes and have

239   more control of the distribution of nests (Schmidt et al. 2001, Schmidt and Ostfeld 2003). These

240   studies demonstrated the hypothesized relationships between (1) GUDs (collected at random

241   locations within the same 2.25 ha plots where artificial nests were deployed) and space use in

242   mice (Fig 4a) and (2) mouse space use and predation of nests by mice (Fig 4b). In contrast, plot-

243   level mouse density failed to predict space use or predation rates on nests. Noteworthy in this

244   regard, Schmidt and Ostfeld (2003) observed 7-fold variation in the amount of space occupied

245   (based on oat grain removal) among the six study plots that in turn varied less than 2-fold in

246   mouse density. Clearly in this example mouse abundance did not scale with their spatial activity,

247   but it was the latter that determined nest predation. Interestingly, annual variation in mouse

248   abundance does predict annual variation in nest success for the ground-nesting veery (*Catharus*

249   *fuscescens*) suggesting that intra-annual spatial variability may be greater than inter-annual

250   variability (Schmidt et al. 2006). Unfortunately, we do not have a temporal sequence of spatial

251   activity or GUDs for comparison to mouse density. However, mouse GUDs were by far the

252   highest recorded at the site in 2000 when mouse populations had collapsed and nest predation

253   rates were their lowest.

254

255   *Spatiotemporal shifts in space use or predation rates* – Whereas the above example focused on

256   spatial variability in QHRs and space use, understanding temporal changes is also important and

257   can be addressed using similar techniques. Schmidt and Whelan (1999) documented a reprieve

258   from nest predation for forest songbirds when a mulberry (*Morus spp.*) mast drew raccoons out

259   of the forest within a suburban arboretum. We were first alerted to this through a drop in nest

260   predation and shift from density-dependent to density independent predation mid-way through an

261   artificial nest study. Artificial nests were replenished daily in the experiment, so intact nests

262   remaining after a night of foraging by raccoons represented a giving-up nest density much the

263   same as seeds remaining in a tray of sand after a bout of foraging. We subsequently

264   demonstrated a concomitant drop in nest predation on shrub-nesting birds (American robin,

265   *Turdus migratorius*, and wood thrush, *Hylocichla mustelina*). Importantly, artificial nest GUDs

266   informed us of current temporal changes in predation rates on real nests. Similarly, Schmidt

267   (2006) showed the density of active veery nests drops as much as 20% or more (due to

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268   predation) between the full and new lunar phases when white-footed mice demonstrated a 3-fold

269   increase in the amount of space occupied (based again on oat grain removal), typical of nocturnal

270   rodents (Kotler et al. 1991, Mandelik et al. 2003, Abramsky et al. 2004). These observations

271   suggest that GUDs can be used as an indicator of temporal shifts in space use/activity and

272   predation rates as alternative resources rapidly renew (or pulse) in the environment, or through

273   rapid temporal variation in predation risk from apex predators. The two studies described above

274   relied on 'natural' GUDs (or standing crop of nests after a night of foraging by raccoons or mice)

275   instead of using artificial food patches. In these cases the experimenter has little control of

276   resource renewal rates that can cloud interpretation of the data (see Morris and Mukherjeee, this

277   volume). But systems such as these should be amenable to the use of artificial food patches for

278   monitoring and understanding the causes and consequences of temporal shifts in predator

279   behavior and predation rates. Raccoon food patches were developed after Schmidt and Whelan's

280   observations (*Berris, unpublished*). Likewise, Schmidt (2006) did attempt to collect mouse

281   GUDs, but artifacts due to playbacks of owl vocalizations interfered with isolating a moon effect

282   (*KAS, unpublished*).

283

284   *Variation in the predator community* – Coexisting consumer species often differ considerably in

285   their giving-up densities; in fact this observation has become a tool in the search for mechanisms

286   of coexistence between competitors (Brown 1989, Kotler and Brown 1999). However, the

287   relevance of interspecific variation in GUDs for species interactions outside of competition has

288   received far less attention. Our model suggests interspecific variation, through effects on space

289   use and predation, can be far-reaching. For instance, Schmidt (unpublished) collected GUDs

290   from both white-footed mice and eastern chipmunks (*Tamias striatus*) foraging in the same food

291   patches that were replenished between nighttime exploitation by mice and daytime exploitation

292   by chipmunks. Mice (20g) had much lower GUDs than the larger bodied, diurnally-active

293   chipmunk (100g). It is unknown whether body mass, metabolic demands or other life history

294   characteristics might lead to a predictable hierarchy of GUDs among species. Regardless, these

295   species differences, based on our modeling approach, predict that mice should exploit a greater

296   amount of space than chipmunks, all else equal (see Fig. 1). If true, two additional predictions

297   follow: (1) mice should cause higher mortality rates on nests than chipmunks (i.e., mice use more

298   space) and (2) given the greater area of space used, mice will show compensatory predation on

299   nests following chipmunk removal, but not vice versa. Both of these predications have been

300   upheld (see Schmidt et al. 2001b and Fig. 5). Unfortunately, Schmidt and Ostfeld (2003) were

301   unable to quantify space use in chipmunks, so the prediction of interspecific differences in space

302   use commensurate with differences GUDs has not been directly tested.

303   The assumption of all 'else equal' certainly doesn't hold in this example, and there are

304   numerous alternative explanations for species differences in nest predation rates. For instance,

305   the artificial nests used by Schmidt et al. (2001b) may not have mimicked real nests in important

306   ways, i.e., chipmunks may use begging calls as cues to locate nests (Haskell 1999). Still, the

307   conclusion we hope the reader takes away is that QHRs/GUDs are an empirical tool as well as

308   the center piece of a larger set of conceptual ideas (e.g., mechanisms of coexistence, foraging

309   ecology, incidental predation) that can be applied to individual species as well as communities.

310   As used here, QHR theory and GUD methodology may provide a useful framework toward

311   understanding the distribution of species interaction strengths within communities, or predicting

312   the consequences, such as additive or non-additive predation resulting from the loss or

313   introduction of predator species.

314

315   *Zero-capture data* – Our colleague, Richard Ostfeld, has maintained six 2.25 ha small mammal

316   trapping grids at IES since 1995. We have used small mammal abundance data from these grids

317   to document temporal trends in nest predation rates on ground-nesting birds, such as the veery.

318   In early studies (Schmidt et al. 2001b) we used crude measures of mouse abundance: minimum

319   number known alive (MNA). These studies were later followed by more sophisticated estimates

320   of plot-level abundance through the program MARK (Schmidt and Ostfeld in press). At the

321   same time, we began using a very crude metric of local activity density - simply quantifying the

322   proportion of trap stations where no mice were captured over the course of a capture season. Not

323   only do these metrics vary in their sophistication, but the field and analytical effort needed to

324   produce each estimate varies considerably. In the end, correlating temporal and spatial

325   variability in mouse abundance/activity to nest predation on two thrush species required only the

326   simplest metric, zero-capture trap data (Schmidt et al. 2006).

327   The proportion of traps with zero mouse captures predicted nest predation in veeries both

328   annually and locally within a 30×30m area (nine trap stations centered on each nest; what we

329   called a nest neighborhood; Fig. 6). Zero-capture data also demonstrated an exponential decline

330   in unused space as predicted from the random territory placement model of Schauber (2000)

331   discussed above. However, the decline reached a plateau, not predicted in the model signifying

332   that even at extreme mouse densities a significant proportion (~10%) of space, on average,

333   remained unoccupied (Schmidt et al. 2006). This method of quantifying predator-free space by

334   enumerating information only from trap stations that record no predator activity (i.e., captures)

335   thus provides a useful surrogate for monitoring spatiotemporal heterogeneity in nest predation

336   rates. In some ways, this should not be surprising. If prey are capable of appropriately

337 responding to predation risk then knowledge of where predators are not may be a more

338 meaningful way to track predation rates since the researcher is attempting to assess predation risk

339 in ways that may be similar to what prey use. In our example, this works even though prey (i.e.,

340 stationary nests) have to 'live' with their choice for 4 weeks. However, if prey were not

341 incidental we suspect predators would quickly respond to the distribution of their prey.

342

343 *Track plates* – When terrestrial predators are identifiable from their tracks, unbaited track plates

344 offer an efficient method to quantify predator activity density at relevant spatial scales without

345 substantially altering predator behavior or their pattern of space use as a result of luring the

346 predator (e.g., traps or cameras baited with food or scent lures; Connors et al. 2005). Connors et

347 al. (2005) designed track plates to use with small mammals by coating acetate transparency

348 sheets with a mixture of graphite powder, mineral oil (for water resistance), and alcohol (carrier).

349 These proved highly effective and convenient for recording tracks and had little evident impact

350 on visitation by white-footed mice (Connors et al. 2005).

351 We used the activity data obtained from track plates to measure the magnitude, spatial

352 scale, and temporal persistence (over periods of months to years) of hot spots and cold spots in

353 mouse activity density (Connors 2005, Schauber et al. in revision). These characteristics appear

354 to be highly relevant to the persistence of gypsy moths in eastern oak forests, where predatory

355 mice are typically abundant and pupal predation rates are high (Campbell et al. 1975, Elkinton et

356 al. 1996, Jones et al. 1998). The vulnerable pupal stage is sedentary and adult female moths are

357 flightless, so egg masses are most likely to be laid in sites of low predation risk (i.e., spatial

358 selection). We found that track activity at a tree was a strong indicator of predation rate on

359 gypsy moth pupae deployed there (Fig. 7).

360   If hot and cold spots of predation persist between years and have spatial scales larger than

361   typical dispersal distances of larvae, then larvae can inherit the level of risk their mothers

362   experienced. This combination of spatial selection and inheritance can reduce overall predation

363   on moth populations below the threshold necessary to cause negative population growth

364   (Schauber et al. 2007). However, estimating predation from either naturally occurring or

365   experimentally deployed pupae would likely yield biased results and actually alter the behavior

366   of the foraging mice (Schauber and Jones 2006). Thus, using track plates to measured predator

367   activity density as an indicator of predation risk was the only feasible way to test our hypotheses

368   by quantifying the persistence and scale of relative refugia.

369   Overall mouse activity decreased greatly between 2004 and 2005, concommittant with a

370   crash in mouse abundance following acorn failure (Connors 2005, Schauber et al. *in revision*).

371   However, only by monitoring the spatial and temporal dynamics of mouse activity were we to

372   fully understand the implications of this crash. Temporal autocorrelation of mouse activity

373   between months was high during years of relatively high mouse density (2003 and 2004),

374   providing stable refugia that prey could exploit, whereas this temporal autocorrelation was

375   considerably lower during the crash year (Connors 2005, Schauber et al. *in revision*). We

376   hypothesize that the increased stability of refugia during periods of high predator density is

377   expected to buffer prey populations from the drastic mast-driven fluctuations that white-footed

378   mouse populations exhibit (Wolff 1996, Ostfeld et al. 1996, McCracken et al. 1999). Such

379   density dependence in space-use stability may arise via greater social stability during periods of

380   high density when summer reproduction is suppressed (Falls et al. 2007), or perhaps just from

381   demographic stochasticity in mouse populations at small spatial scales when overall density is

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382   low. These mechanisms are ripe for future empirical investigation, and highlight the

383   insufficiency of predator population density as a sole indicator of risk to prey.

384

385   **Concluding remarks** – Our conceptual approach centers on an animal's quitting harvest rate for

386   two reasons. First, mechanistically both space use and time devoted to foraging any particular

387   patch are related to the QHR and patterns of adaptive foraging as developed above. Second, the

388   QHR (or GUD) is a phenomenological outcome of a predator's assessment of its foraging costs

389   and benefits (Brown 1988, Brown and Kotler 2004). The QHR thus presents a window into the

390   world of a predator by reflecting its ecological relationships with its environment, such as its

391   energetic state (influenced by its density and the availability of primary prey), the instantaneous

392   risk of predation from apex predators, and current valuation of food and safety. QHRs/GUDs

393   thereby incorporate the influence of multiple trophic levels (Fig. 1) and may provide a more

394   informative and causal link to space use and rates of predation (i.e., strength of species

395   interactions) than predator density would by itself. GUDs can also reveal the operation of

396   density dependence (see Morris and Mukherjee 2007). For instance, changes in population

397   density of the predator may manifest as a foraging cost (mainly the marginal value of energy

398   increases with density, as resources are depleted; Schmidt et al. 2004) that can be observed

399   through changes in QHRs and GUDs (Bowers et al. 1993, Davidson and Morris 2001, Morris

400   and Mukherjee 2007). As with any ecological model, the set of linkages depicted in Fig. 3

401   represent a subset of those that actually exist, and some classes of predators may not reasonably

402   fit within the current conceptualization. Nonetheless, we believe the model generalizes a broad

403   and important group of interactions characterizing predator-prey interactions that fall within the

404   purview of incidental predation. It also provides a cornerstone to conceptualizing behavioral

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405   mechanisms that anchor predators in space, such as territoriality and central place foraging, that

406   are likely to generalize to both incidental and non-incidental prey (e.g., wolf-deer interactions;

407   Mech 1977).

408   Although monitoring GUDs reveals insights into the costs and benefits of foraging, the

409   use of artificial food patches to collect GUDs may not reveal predation risk for prey at any

410   specific point, whereas quantifying activity density may. For instance, collecting GUDs in a

411   forested landscape to monitor nest predation levels might tell us that predator space use and

412   predation risk (on nests) in the environment is low but GUDs alone cannot reveal which

413   individual songbird nests (or other prey) are most at risk because overall levels of predation risk

414   and missed opportunity both manifest at large spatial scales. For example, abundant food

415   elsewhere in an animal's territory will influence GUDs collected at a point source (Brown and

416   Alkon 1990, Schmidt et al. 2001a). Likewise, GUDs collected at a relatively risk-free (from the

417   predator's perspective) point in space but in an otherwise high risk environment would fail to

418   accurately reveal the mean likelihood incidental predation outside local site where GUDs were

419   collected. Alternatively, demographic inertia could cause the spatial and temporal distributions

420   of activity of predators to imperfectly reflect the distribution of habitat quality (Schauber et al in

421   revision). Quantifying activity density concomitantly with GUDs can enable researchers to

422   disentangle and compare the landscape of risk experienced by prey (determined by activity

423   density of predators) with the landscape of forging costs experienced by the predator.

424   It was our goal to promote the use of behavioral indicators as an effective tool to increase

425   our understanding of predator-prey interactions, not as a substitute for measuring abundances

426   and other population-level characteristics. A detailed field study of breeding birds will

427   accurately measure nest predation rates, take video images of nest predators, and collect data on

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428   avian demography and possible information on site and individual variation in quality to monitor

429   processes such as density-dependence in reproductive success. Yet many studies or basic

430   monitoring schemes have more modest goals. Even if money is no objective, detailed field

431   studies of breeding populations cannot estimate nest predation in advance of the breeding season

432   - within season estimates will be too late to implement management programs intent on boosting

433   reproductive productivity. In contrast, GUDs and activity density can be collected prior to the

434   breeding season to monitor predator behavior or as surrogates for nest predation rates. Lastly,

435   GUDs and activity density can greatly increase the cost-effectiveness of conservation efforts,

436   particularly in poor nations that cannot mount an effective field effort to monitor avian

437   reproductive ecology and nest predator behavior. Outside of monitoring actual predation events

438   (artificial nests or video images from real nests) the predator has largely been absent from nest

439   predation studies, although some excellent examples exist (e.g., Vigallon and Marzluff 2005).

440   GUDs and activity density are complementary and cost-effective indicators of the "worlds" that

441   predators and their prey inhabit.

442

443   **ACKNOWLEDGEMENTS**

451 behavioral indicators, but most of all of their vision and leadership for bridging behavioral

452 ecology and conservation.

453

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580 **FIGURE LEGENDS**

581 Figure 1. A simplified framework for viewing the operation of patch-use based interactions on

582 prey mortality through the predator. Predator-free or predator-poor space arises through bottom-

583 up and top-down factors that influence the predator's QHR. The QHR is an integrative measure

584 that is influence by, among other factors not shown, the predator's density, and the abundances

585 of primary food and predation risk from apex predators. When possible, we indicate the likely

586 relationship(s) (0, +, -) between two factors when the first is increased, e.g., increasing the QHR

587 creates more behavioral refugia and reduces foraging time.

588

589 Figure 2. Creation of nest predator-free space and consequences for incidental prey, i.e.,

590 passerine nests. There are two ways to interpret the figure (i) bottom-up and (ii) top-down

591 creation. In (i) local primary prey density decreases from blue to red contour lines, whereas risk

592 of attack from apex predators is homogeneous throughout the environment. The predator has a

593 fixed quitting harvest rate (QHR) that increases from panel (a) → (c). Predator-free space is

594 shown by removing contour lines in panels (b) and (c); i.e., predator-free space occurs where

595 local resource abundance < QHR. A higher QHR creates more predator-free space and fewer

596 nests are vulnerable to predation.

597

598 Alternatively, in (ii) contour lines indicate increasing (blue to red) QHR due to local risk from

599 apex predators, whereas the abundance of primary prey is homogeneous throughout the

600 environment. Primary prey abundance

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602   In either case, In nature both scenarios are likely to apply simultaneously; the difference is

603   whether one conceives of spatial heterogeneity created primarily through the distribution or

604   reward (i) or risk (ii). In all cases, predator-free space occurs where local primary prey densities

605   falls below the predator's local QHR. Increasing the QHR changes the distribution and

606   decreases the abundance of predator-free space, which is especially important for incidental prey

607   such as songbird nests (represented by the clutch of eggs). Maybe we should just stick to

608   illustrating bottom-up creation since I am finding it hard to illustrate both in simple terms that

609   will avoid confusion. Ignore the highlighted section if that the case.

610

611   Figure 3. (A) Proportion of space used and (B) prey consumption as a function of a predator's

612   giving-up density (GUD) in a simulated landscape produced in MATLAB. Primary (n=1000)

613   and incidental (n=50) prey were randomly and independently assigned to one of 100 patches

614   (this produces a Poisson distribution of prey). Only patches with initial primary prey quality >

615   GUD were foraged, and of these final prey density = GUD. Random search time for a given

616   foraged patch (i) was calculated as: $t_i = (1/a_p) \log (N_i/GUD)$, where a_p is the encounter rate on

617   primary prey and N_i and GUD are, respectively, the initial and final number of primary prey in

618   patch (i). The probability, I_p, an individual incidental prey item was consumed from a foraged

619   patch was calculated as: $I_p = [1-e^{(-a_i t_i)}]$. Actual incidental prey consumption was determined by

620   comparing I_p to a random number (uniform distribution). Figure shows the mean results from

621   1000 simulations at each specified GUD. $a_p = 0.6$, $a_i = 0.6$.

622

623   Figure 4. Relationships between (A) space use (quantified as the proportion oat grains removed

624   by mice off a lattice grid arrangement) and mouse giving-up density (log-transformed) and (B)

27

625   the percentage of nests depredated by mice and space use. Each data point represents one of six

626   2.25 ha plots from which the data were collected. See Schmidt and Ostfeld (2003) for more

627   details of the experimental methods. Figures reprinted with permission from Schmidt and

628   Ostfeld (2003).

629

630   Figure 5. Artificial nest daily mortality rates (DMRs = number of nest depredated/nest exposure

631   days; after Mayfield 1975) as a function of rodent abundance. (A) Per capita nest DMR (log-

632   transformed) specific to mice (solid circles) or chipmunks (open circles) as determined by incisor

633   marks on clay eggs. Each data point represents one of six 2.25 ha plots from which the data

634   were collected (3 plots omitted for mice due to an experimental mouse removal). (B) Overall

635   (all predators included) nest DMRs (± SE) on control (n=3) or removal (n=3) plots; mice were

636   removed in 1997, chipmunks in 1998). See Schmidt et al. (2001a) for more details of the

637   experimental methods. Figures reprinted with permission from Schmidt et al. (2001a).

638

639   Figure 6. Veery nest success (proportion of nests fledged) as a function of zero-capture data:

640   proportion of the 9 traps stations comprising a trap neighborhood that recording zero mouse

641   captures during spring-summer trapping sessions; see Schmidt et al. 2006 for more details).
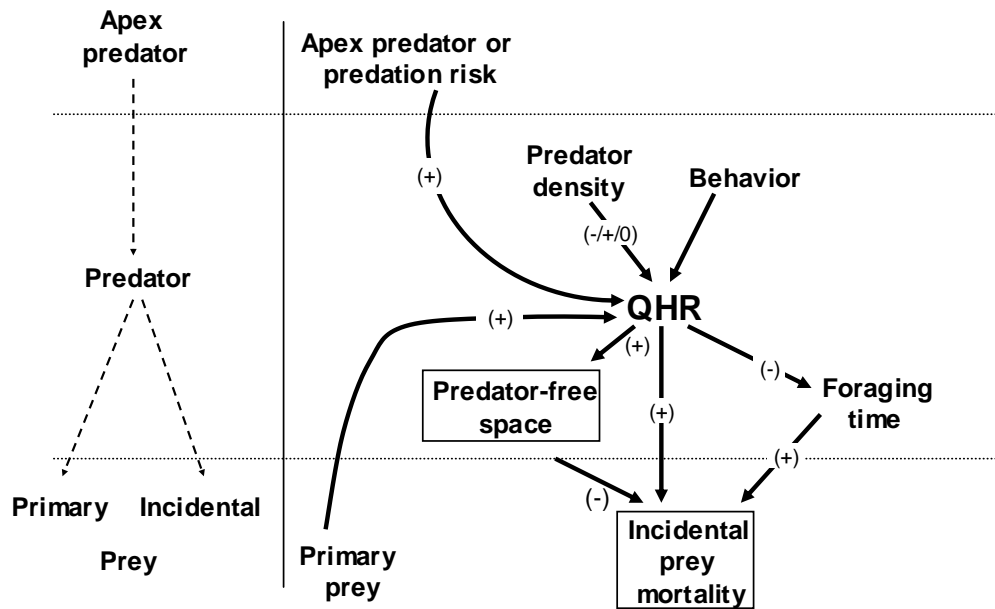
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643   Figure 7. Mean (+ SE) daily predation of gypsy moth pupae deployed on (1.5 m height) or at the

644   base of (ground) trees, as a function of the percentage of track plates recording mouse tracks at

645   those trees over a 10-12 day period at the Institute of Ecosystem Studies, Millbrook, New York,
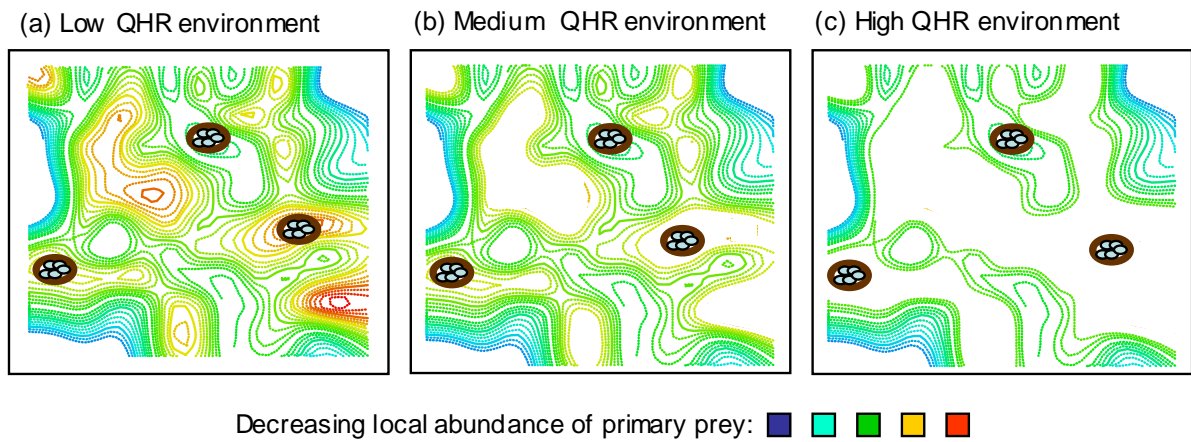
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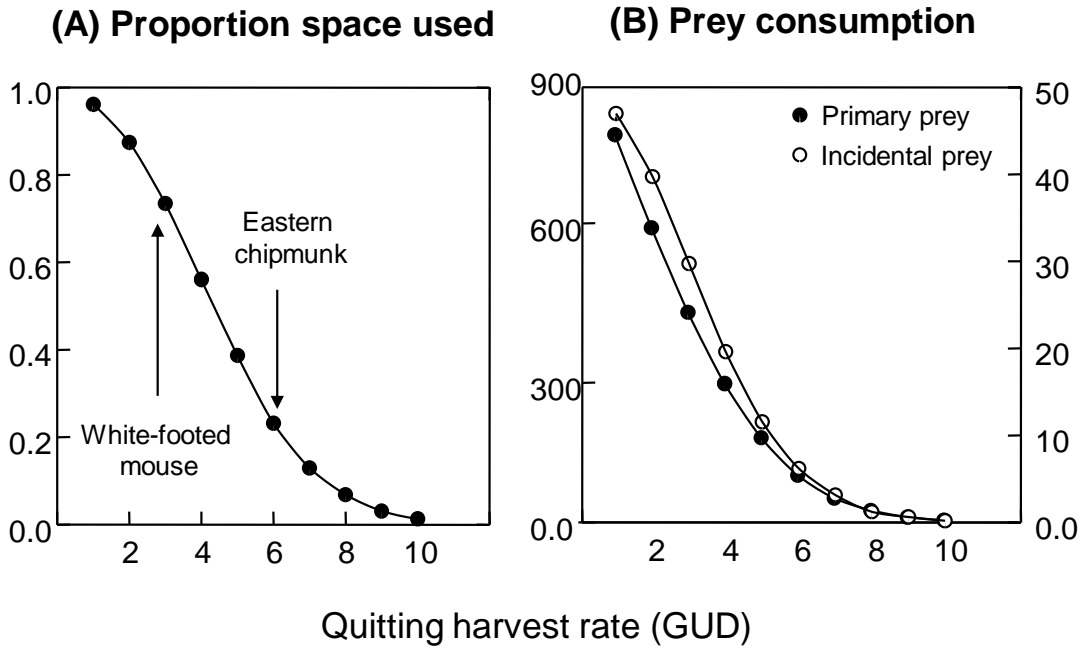649   **FIG. 1**
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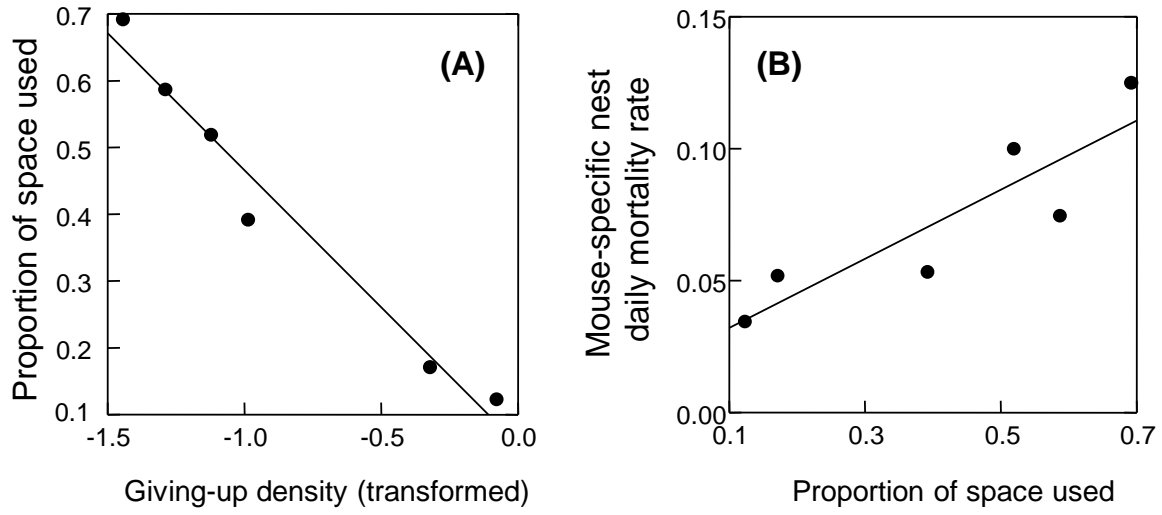659 **FIG. 2**
660 NO REFERENCE TO FIG 2 IN TEXT
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(a) Low QHR environment   (b) Medium QHR environment   (c) High QHR environment

Decreasing local abundance of primary prey: ◼ ◼ ◼ ◼ ◼

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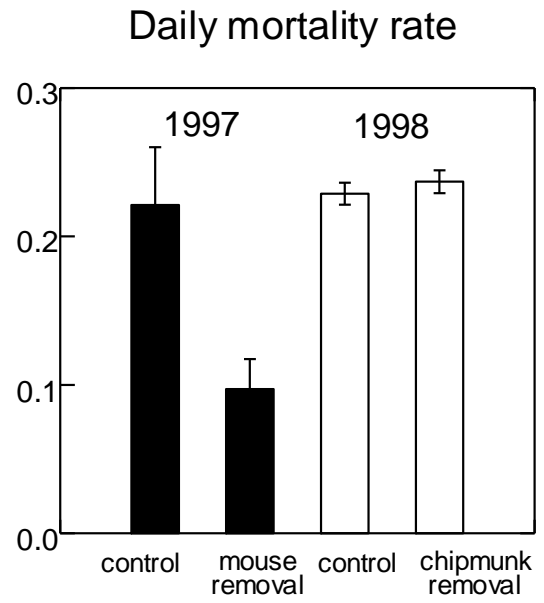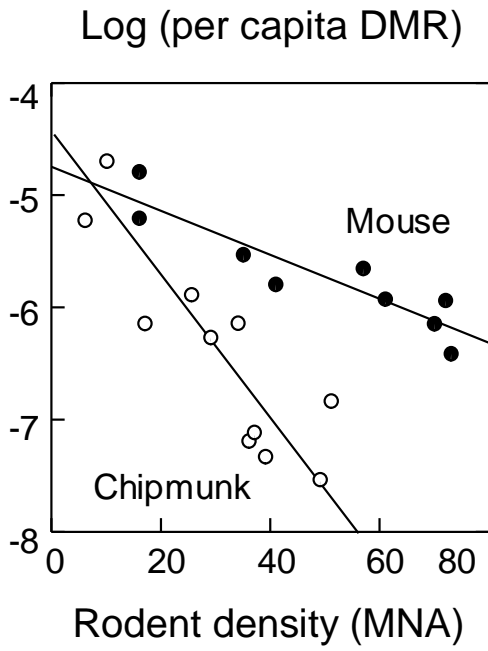665   **FIG. 3**
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(A) Proportion space used   (B) Prey consumption

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670 **FIG. 4**
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693 **FIG. 6**
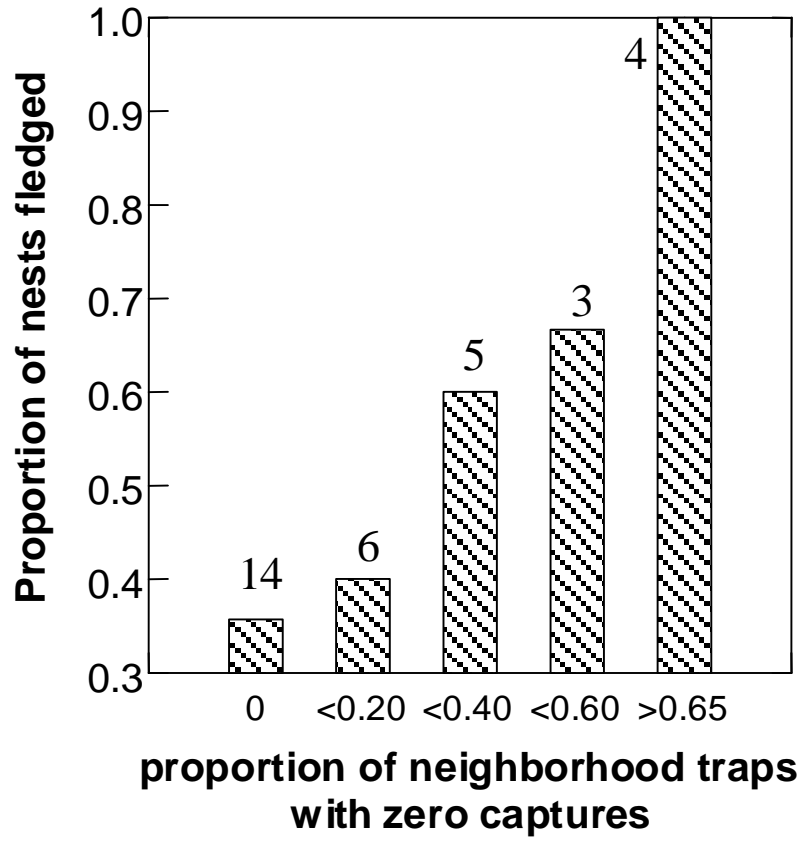694
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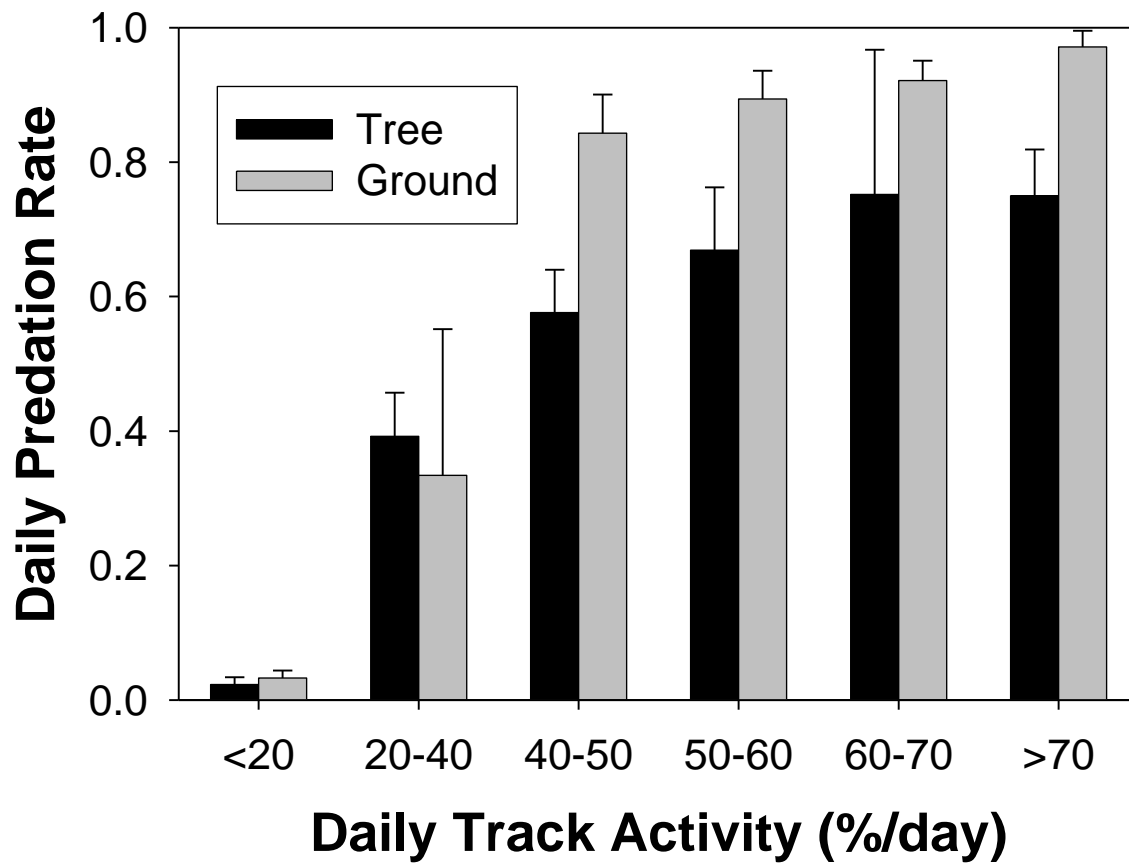696
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707   Fig. 7

Daily Predation Rate vs **Daily Track Activity (%/day)**

Legend: ■ Tree ■ Ground

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710   LITERATURE CITED
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