November 2006

Trapping *Phyllophaga* spp. (Coleoptera: Scarabaeidae: Melolonthinae) in the United States and Canada using sex attractants.

Paul S. Robbins
Cornell University, Ithaca, NY

Steven R. Alm
Univ. of Rhode Island, Kingston, RI

Charles D. Armstrong
Univ. of Maine, Orono, ME

Anne L. Averille
Univ. of Massachusetts, Amherst MA

Thomas C. Baker
Pennsylvania State Univ., University Park, PA

See next page for additional authors

Authors

Paul S. Robbins, Steven R. Alm, Charles D. Armstrong, Anne L. Averille, Thomas C. Baker, Robert J. Bauernfiend, Frederick P. Baxendale, S. Kris Braman, Rick L. Brandenburg, Daniel B. Cash, Gary J. Couch, Richard S. Cowles, Robert L. Crocker, Zandra D. DeLamar, Timothy G. Dittl, Sheila M. Fitzpatrick, Kathy L. Flanders, Tom Forgatsch, Timothy J. Gibb, Bruce D. Gill, Daniel O. Gilrein, Clyde Gorsuch, Abner M. Hammond, Patricia D. Hastings, David W. Held, James L. Holliman, William G. Hudson, Michael G. Klein, Vera L. Krischik, David J. Lee, Charles E. Linn Jr., Nancy J. Luce, Kenna MacKenzie, Catherine M. Mannion, Sridhar Polavarapu, Daniel A. Potter, Daniel A. Potter, Wendell Roelofs, Brian M. Royals, Glenn A. Salsbury, Nathan M. Schiff, David J. Shetlar, Margaret Skinner, Beverly L. Sparks, Jessica A. Sutschek, Timothy P. Sutschek, Stanley R. Swier, Martha M. Sylvia, Neil J. Vickers, Patricia A. Vittum, Richard Weidman, Donald C. Weber, R. Chris Williamson, and Michael G. Villani

Trapping *Phyllophaga* spp. (Coleoptera: Scarabaeidae: Melolonthinae) in the United States and Canada using sex attractants.

Paul S. Robbins[1,*], Steven R. Alm[2], Charles. D. Armstrong[3], Anne L. Averill[4], Thomas C. Baker[5], Robert J. Bauernfiend[6], Frederick P. Baxendale[7], S. Kris Braman[8], Rick L. Brandenburg[9], Daniel B. Cash[10], Gary J. Couch[11], Richard S. Cowles[12], Robert L. Crocker[13], Zandra D. DeLamar[14], Timothy G. Dittl[15], Sheila M. Fitzpatrick[16], Kathy L. Flanders[14], Tom Forgatsch[17], Timothy J. Gibb[18], Bruce D. Gill[19], Daniel O. Gilrein[20], Clyde S. Gorsuch[21], Abner M. Hammond[22], Patricia D. Hastings[23], David W.Held[24], Paul R. Heller[5], Rose T. Hiskes[12], James L. Holliman[25], William G. Hudson[26], Michael G. Klein[27], Vera L. Krischik[28], David J. Lee[29], Charles E. Linn, Jr.[1], Nancy J. Luce[4], Kenna E. MacKenzie[30], Catherine M. Mannion[31], Sridhar Polavarapu[32,†], Daniel A. Potter[33], Wendell L. Roelofs[1], Brian M. Royals[9], Glenn A. Salsbury[34], Nathan M. Schiff[35], David J. Shetlar[36], Margaret Skinner[37], Beverly L. Sparks[38], Jessica A. Sutschek[39], Timothy P. Sutschek[39], Stanley R. Swier[40], Martha M. Sylvia[41], Neil J. Vickers[42], Patricia J. Vittum[4], Richard Weidman[23], Donald C. Weber[43], R. Chris Williamson[44] and Michael G Villani[1,†]

[1] Cornell Univ., New York State Agric. Experiment Station, Geneva, NY psr1@cornell.edu, cel1@cornell.edu, wlr1@cornell.edu
[2] Univ. of Rhode Island, Kingston, RI stevealm@uri.edu
[3] Univ. of Maine, Orono, ME charlesa@umext.maine.edu
[4] Univ. of Massachusetts, Amherst MA aaverill@ent.umass.edu, nluce@psis.umass.edu, pvittum@ent.umass.edu
[5] Pennsylvania State Univ., University Park PA tcb10@psu.edu, prh@psu.edu
[6] Kansas State Univ., Manhattan, KS rbauernf@oz.oznet.ksu.edu
[7] Univ. of Nebraska, Lincoln NE fbaxendale1@unl.edu
[8] Georgia Experiment Station, Griffin, GA kbraman@griffin.uga.edu
[9] North Carolina State Univ., Raleigh, NC rick_brandenburg@ncsu.edu, brian_royals@ncsu.edu
[10] Franklinville, NY dbcash@cnyti.com
[11] Cornell Univ. Cooperative Extension, Middletown, NY gjc15@cornell.edu
[12] Connecticut Agricultural Experiment Station, Windsor, CT richard.cowles@po.state.ct.us,
[13] Texas Department of Agriculture, Austin, TX robert.crocker@agr.state.tx.us
[14] Auburn Univ., Auburn, AL zd289coupe@yahoo.com, flandkl@auburn.edu
[15] Ocean Spray Cranberries, Babcock, WI tdittl@oceanspray.com
[16] Agriculture & Agri-Food Canada, Agassiz, British Columbia, Canada fitzpatricks@agr.gc.ca
[17] Bandon, OR osonegro@peoplepc.com
[18] Purdue Univ., West Lafayette, IN gibb@purdue.edu

[19] Center for Plant Quarantine Pests, Ottawa, Canada gillbd@inspection.gc.ca
[20] Cornell Univ. Cooperative Extension, Riverhead, NY dog1@cornell.edu
[21] Clemson Univ., Clemson, SC csgorsuch@att.net
[22] Louisiana State Univ., Baton Rouge, LA ahammond@agcenter.lsu.edu
[23] Rutgers Univ. Cooperative Extension, New Brunswick, NJ hastings@aesop.rutgers.edu, weidman@rcre.rutgers.edu
[24] Mississippi State Univ, Biloxi, MS dwh56@ra.msstate.edu
[25] Alabama Agricultural Experiment Station, Marion Junction, AL jhollima@acesag.auburn.edu
[26] Univ. of Georgia, Tifton, GA wghudson@uga.edu
[27] Ohio State Univ., Wooster, OH klein.10@osu.edu
[28] Univ. of Minnesota, St. Paul, MN krisc001@tc.umn.edu
[29] New York State Tree Nursery, Saratoga Springs, NY djlee@gw.dec.state.ny.us
[30] Agriculture & Agri-Food Canada, Kentville, Nova Scotia, Canada mackenziek@agr.gc.ca
[31] Univ. of Florida, Homestead, FL cmannion@mail.ifas.ufl.edu
[32] Rutgers Univ., Blueberry and Cranberry Research Center, Chatsworth, NJ
[33] Univ. of Kentucky, Lexington, KY dapotter@uky.edu
[34] Kansas Department of Agriculture, Greensburg, KS gsalsbury@sbcglobal.net
[35] USDA Forest Service, Stoneville, MS nschiff@asrr.arsusda.gov
[36] Ohio State Univ., Columbus, OH shetlar.1@osu.edu
[37] Univ. of Vermont, Burlington, VT margaret.skinner@uvm.edu
[38] Univ. of Georgia, Athens, GA bsparks@uga.edu
[39] Tarpon Springs, FL jessie_sutschek@yahoo.com
[40] Univ. of New Hampshire, Durham, NH stan.swier@unh.edu
[41] Univ. of Massachusetts Cranberry Experiment Station, Wareham,MN martys@umext.umass.edu
[42] Univ. of Utah, Salt Lake City, UT vickers@biology.utah.edu
[43] USDA-ARS, Beltsville, MD weberd@ba.ars.usda.gov
[44] Univ. of Wisconsin, Madison, WI rcwillie@entomology.wisc.edu
[†] Deceased - Sridhar Polavarapu and Michael Villani are greatly missed by family, friends, and colleagues.

Abstract

The sex pheromone of the scarab beetle, *Phyllophaga anxia*, is a blend of the methyl esters of two amino acids, L-valine and L-isoleucine. A field trapping study was conducted, deploying different blends of the two compounds at 59 locations in the United States and Canada. More than 57,000 males of 61 *Phyllophaga* species (Coleoptera: Scarabaeidae: Melolonthinae) were captured and identified. Three major findings included: (1) widespread use of the two compounds [of the 147 *Phyllophaga* (*sensu stricto*) species found in the United States and Canada, males of nearly 40% were captured]; (2) in most species intraspecific male response to the pheromone blends was stable between years and over geography; and (3) an unusual pheromone polymorphism was described from *P. anxia*. Populations at some locations were captured with L-valine methyl ester alone, whereas populations at other locations were captured with L-isoleucine methyl ester alone. At additional locations, the L-valine methyl ester-responding populations and the L-isoleucine methyl ester-responding populations were both present, producing a bimodal capture curve. In southeastern Massachusetts and in Rhode Island, in the United States, *P. anxia* males were captured with blends of L-valine methyl ester and L-isoleucine methyl ester.

Resumen

La feromona sexual del escarabajo, *Phyllophaga anxia,* es una mezcla de los ésteres metílicos de dos aminoácidos, L-valina y L-isoleucina. Se condujo un estudio de campo usando diferentes mezclas de los dos componentes en 59 sitios de Estados Unidos y Canada. Más de 57,000 machos de 61 especies de *Phyllophaga* fueron capturados e identificados. Tres de los resultados más importantes incluyen: (1) el extenso uso de los dos componentes [de las 147 especies de *Phyllophaga* (*sensu stricto*), en Estados Unidos y Canada, fueron capturados machos de cerca del 40% de ellas.]; (2) para la mayoría de las especies, la respuesta intraespecífica de los machos a las combinaciones de los dos aminoácidos fue consistente entre años diferentes, y en todos los sitios geográficos; y (3) un inusual polymorfismo de la feromona fue descrito para *P. anxia*. Poblaciones de algunos sitios fueron atrapados sólo con valina, mientras que poblaciones de otros sitios fueron atrapados sólo con isoleucina. También se encontraron sitios donde las poblaciones responden a ambos componentes, valina e isoleucina, produciendo una curva de captura bimodal. En el sureste del estado de Massachusetts y en Rhode Island, en Estados Unidos, machos de *P. anxia* fueron atrapados en trampas con mezclas de valina e isoleucina.

Correspondence: *psr1@cornell.edu
Received 12.10.2006 | Accepted 14.2.2006 | Published: 15.11.2006

ISSN: 1536-2442 | Volume 6, Number 39

Cite this paper as:
Robbins PS, Alm SR, Armstrong CD, Averill AL, Baker TC, Bauernfiend RJ, Baxendale FP, Braman SK, Brandenburg RL, Cash DB, Couch GJ, Cowles RS, Crocker RL, DeLamar ZD, Dittl TG, Fitzpatrick SM, Flanders KL, Forgatsch T, Gibb TJ, Gill BD, Gilrein DO, Gorsuch CS, Hammond AM, Hastings PD, Held DW, Heller PR, Hiskes RT, Holliman JL, Hudson WG, Klein MG, Krischik VL, Lee DJ, Linn Jr. CE, Luce NJ, MacKenzie KE, Mannion CM, Polavarapu S, Potter DA, Roelofs WL, Royals BM, Salsbury GA, Schiff NM, Shetlar DJ, Skinner M, Sparks BL, Sutschek JA, Sutschek TP, Swier SR, Sylvia MM, Vickers NJ, Vittum PJ, Weidman RB, Weber DC, Williamson RC, Villani MG. 2006. Trapping *Phyllophaga* spp. (Coleoptera: Scarabaeidae: Melolonthinae) with sex attractants in the United States and Canada. 124pp. *Journal of Insect Science* 6:39, available online: insectscience.org/6.39.

Introduction

The scarab beetle genus *Phyllophaga* (*sensu lato*) is one of the largest genera of animals in the United States (Woodruff and Beck 1989), encompassing 203 described species in 8 subgenera, including 147 species (and 8 subspecies) in the subgenus *Phyllophaga* (*sensu stricto*), 39 species in *Listrochelus*, 7 species in *Phytalus*, 3 species in *Cnemarachis* (all non-native and confined to south Florida), 3 species in *Eugastra*, 2 species in *Tostegoptera*, 1 species in *Chlaenobia*, and 1 species in *Triodonyx* (Evans 2003, Smith and Evans 2005). Their striking genitalic morphology, first described in the late 19th century (Smith 1888), continues to be the most important taxonomic character used to separate species in this group (Luginbill and Painter 1953). See Woodruff and Beck (1989) and Woodruff and Sanderson (2004) to view excellent scanning electron microscopy images of *Phyllophaga* genitalia.

The economic importance of this genus relates principally to the root feeding habits of the larvae, commonly called white grubs. Larvae of various species of *Phyllophaga* have been recorded feeding on crops that include, but are not limited to, nursery stock (Andre 1937), corn (Bessin 1999), commercial turfgrass (Brandenburg and Villani 1995; Vittum et al. 1999), cranberries (Dunn and Averill 1996; Eck 1990; Franklin 1950), sugarcane (Gordon and Anderson 1981), sweet potato (Hammond et al. 1997), and pasture (Luginbill and Painter 1953). True to the Greek origin of their generic name (*Phyllo*-leaf + *phaga*-eat), adult *Phyllophaga* in very large flights have been known to defoliate stands of trees. Although adults of some *Phyllophaga* species are apparently host specific, most are polyphagous (Luginbill and Painter 1953).

P. anxia (LeConte) is the most widely distributed *Phyllophaga* species in North America (Luginbill and Painter 1953; Woodruff and Beck 1989). Two genitalic morphs are described in this species, the northern form and the southern form (Luginbill and Painter 1953; Woodruff and Beck 1989). The first sex pheromone described from the genus *Phyllophaga* was identified from virgin *P. anxia* adults dug in mid-April from a cranberry bog in Carver, Massachusetts, before their May flight. The female-produced sex pheromone was determined to be a 75/25 blend of L-valine methyl ester and L-isoleucine methyl ester (Zhang et al. 1997). L-isoleucine methyl ester was first elucidated from *Holotrichia parallela* (Leal et al. 1992), an Asian melolonthine species. *Holotrichia* is regarded by some as being inseparable taxonomically from the Nearctic *Phyllophaga* (Saylor 1937; Saylor 1939).

L-valine methyl ester and L-isoleucine methyl ester are unusual pheromone compounds in that their precursors are the essential amino acids, L-valine and L-isoleucine. These essential amino acids are available only via sequestration from food plants fed on by the larvae, or perhaps from endo-symbionts. Our future investigations will hopefully determine the source of these amino acids. For the most recent overview of beetle semiochemicals see Francke and Dettner (2005).

Since *P. anxia* is a common species throughout the Northeast, the pheromone was deployed in the field near Geneva, New York, in 1996. *P. anxia* males were captured with this blend, as expected. However, another species of *Phyllophaga*, *P. futilis*, was also captured in the traps in much smaller numbers. Our interest was piqued by the *P. futilis* catches because sex pheromones are generally regarded as species-specific mate recognition signals, although studies have demonstrated varying degrees of pheromone specificity between closely related species (Roelofs 1978), as well as pheromone polymorphism in geographically separated conspecifics such as *Agrotis segetum* (Wu et al. 1999), *Ostrinia nubilalis* (Glover et al. 1991; Klun and Cooperators 1975), and *Hemileuca eglanterina* (McElfresh and Millar 2001). Since *P. anxia* is a common species throughout most of North America, this finding presented an opportunity to examine the response specificity of different populations of *P. anxia*, as well as responses of other *Phyllophaga* species, over a large geographic region.

Materials and Methods

Vane traps baited with various blends of L-valine methyl ester and L-isoleucine methyl ester were deployed at 59 different locations in the U.S. and Canada during the years 1996–2001 (Figure 1). At each of these locations, traps were maintained for one to four seasons. Tables 1a and 1b list the trap locations, years during which traps were deployed, and a brief note about the habitat. The trapping sites in Carver, Lakeville, and Plympton, Massachusetts; Chatsworth, New Jersey; Babcock, Wisconsin; Lincolnville Center, Maine; Aggasiz, British Columbia; and Bandon, Oregon, were chosen because the traps could be located adjacent to cranberry acreage. Researchers involved in studies of *Phyllophaga* infesting turf, pasture, nursery, or other commodities maintained some trapping sites. Other sites were selected because it was likely that they might harbor different *Phyllophaga* species from those in other geographic areas and where the lures had never been tested.

When blends are referred to in this study, it is in the ratio of L-valine methyl ester/L-isoleucine methyl ester. In 1996, five blends were deployed, including 100% L-valine methyl ester, 65/35, 50/50, 35/65, and 100 % L-isoleucine methyl ester. In 1997 and 1998, 95/5 and 5/95 blends were added to the array. In 1999, 2000, and 2001, the eight blends tested included 100% L-valine methyl ester, 90/10, 80/20, 60/40, 40/60, 20/80, 10/90, and 100% L-isoleucine methyl ester. In 1996, the lures were produced in our own laboratory by loading 5 mm rubber stopper septa (Thomas Scientific, www.thomassci.com/index.jsp) with 3 mg each of various blends using hexane as the solvent. From 1997 to 2001, Dr. A.C. Oehlschlager of ChemTica Internacional S.A. (San Jose, Costa Rica, www.chemtica.com) generously supplied the rubber septa lures for the tests. During that time, the lures were loaded with 4 mg of the various blends. At each location a control trap with a blank septum also was deployed.

In 1996 and 1997, the traps used in the study were either Trécé Japanese beetle vane traps (Trécé Incorporated, www.trece.com/) or Fuji Flavor Company vane traps (Fuji Flavor Company, www.fjf.co.jp/). Beginning in the 1998 season, vane traps were fabricated in the laboratory from three-liter soda bottles and 4 mm white corrugated plastic (Figure 2). When removed from the field during the winter, these traps lasted up to three field seasons.

Traps were set in the field 15–20 meters apart and at heights of 1–2 meters. The traps were checked and re-randomized one to three times each week. Captured beetles were bagged and frozen, or infrequently preserved in ethanol. Plastic bags or bottles marked with the catch date and blend were shipped at the completion of the trapping period to Geneva, NY, for identification.

Phyllophaga species identifications were assigned using a number of published sources (Luginbill and Painter 1953;Ratcliffe 1991;Riley 1988, Saylor 1939; Saylor 1940; Woodruff and Beck 1989), comparisons with *Phyllophaga* species in the Cornell University insect collection, and consultations with and verifications by E. Richard Hoebeke (Cornell University, Ithaca, NY), Dr. Paul Lago (University of Mississippi, University, MS), Edward C. Riley (Texas A & M University, College Station, TX), and William B. Warner (Farnam Companies, Inc., Phoenix, AZ). In 1998, Dr. Robert Crocker (then at Texas A & M University, Dallas, TX) did identifications of the Texas catch and sent the results to Geneva NY. In 2000 and 2001, Dr. Robert Bauernfiend (Kansas State University, Manhattan, KS) did the same for the Manhattan, Kansas catches. Whenever possible, a series of each species from the various locations was pinned for later vouchering in the Cornell University insect collection.

Results and Discussion

General observations

The following outline condenses the large number of figures and tables found in this publication into general groupings for the convenience of the reader.

Table or Figure	Description of Table or Figure
Tables 1a and 1b	Trapping locations, years, and description of trapping sites
Tables 2a and 2b	Trap catches, arranged alphabetically by species
Tables 3a and 3b	Trap catches by the number caught of each species, descending
Tables 4a and 4b	Trap catches by number of sites where each species was caught
Tables 5-97	Catches at individual locations
Table 98	Synchronically flying species captured by similar sex attractant blends
Figure 1	Geographic locations of all trapping sites
Figure 2	Photo of trap
Figures 3-63	Maps of species distributions and where caught in this study
Figures 64-126	Male sex attractant capture curves, arranged alphabetically by species
Figure 127	*Phyllophaga* male sex attractant response curves, general observations
Figure 128	Sympatric and synchronic flights to different sex attractant blends
Figure 129	Sympatric and asynchronic flights to the same sex attractant blend
Figure 130	Sympatric and synchronic flights to the same sex attractant blend
Figure 131	Seasonal flights of all species - Kansas, Manhattan, 2001
Figure 132	Seasonal flights of all species - Kentucky, 2000
Figure 133	Seasonal flights of all species - Massachusetts, Amherst, 1999
Figure 134	Male *P. anxia* capture curve - L-valine methyl ester responders
Figure 135	Male *P. anxia* capture curve - L-isoleucine methyl ester responders
Figure 136	Male *P. anxia* capture curve - bimodal site
Figure 137	Male *P. anxia* capture curve - blend responders
Figure 138	Map of all sites where *P. anxia* was found and male capture curves

A total of 57,129 *Phyllophaga* individuals were examined and identified in the course of this study. The 215 captured females represented only 0.38% of the total catch, suggesting that the attractants do not function as aggregation pheromones in any of the species. A total of 145 males were counted from the control traps, amounting to only 0.25% of the total catch.

No *Phyllophaga* beetles were captured in Aggasiz, British Columbia; Bandon, Oregon; or Homestead, Florida. In British Columbia and Oregon, the traps were located at cranberry bogs. A light trap operated at the Oregon cranberry bog site also captured no *Phyllophaga*. Despite extensive sampling for root weevils in northwest commercial cranberry bogs, no white grubs have been reported (D. C. Weber, unpublished data). Moreover, when the *Phyllophaga* species distribution maps in Luginbill and Painter (1953) are examined, only four species of *Phyllophaga* are found listed from Oregon. Regarding the Homestead, Florida site, Woodruff (1961) indicates that very few of the Florida *Phyllophaga* species occur in Miami or in the Florida Keys. In the same publication, he points out that “The soil in the Miami area is extremely shallow and underlain by öolitic limestone and, in general, is not a good soil for white grubs.” Only 4 of the 42 species of *Phyllophaga* recorded from Florida have been collected in that area.

Tables 2a and 2b list alphabetically the *Phyllophaga* species captured, the number of males captured in each species, the number of discrete locations at which they were captured, and the total number of site-years for each species [site-years = (site A x number of years that species was captured at that site) + (site B x number of years that species was captured at that site) + ...]. Tables 3a and 3b are sorted by descending catch numbers, beginning with the *Phyllophaga* species caught in the greatest number. Tables 4a and 4b are sorted by site, listing in descending order the number of sites at which a particular species was recorded.

Of all site-years when and where beetles were captured, only two (NJ Chatsworth #2, 1999 Table 59 and UT Salt Lake City, 1999, Table 91) recorded a single species of *Phyllophaga* during a flight season. The average number of species captured during a site-year was 4.15. Three sites (AL Auburn, 1998, Table 6; KS Manhattan #1, 2000, Table 27; and KS Manhattan #2, 2001, Table 28) recorded more than 10 species of *Phyllophaga* captured during the flight season.

The species that was taken in the greatest number (20,480), in the greatest number of sites (33), and in the greatest number of site-years (54) was *P. anxia*. This is not surprising given that, as was indicated previously, it is the most widespread species of *Phyllophaga* in North America. Luginbill and Painter (1953) list it as occurring in every state in the United States except Arizona, California, Florida, Nevada, West Virginia, and Wyoming. They also report *P. anxia* from all ten Canadian provinces. Woodruff and Beck (1989) have subsequently reported it from Florida. W. B. Warner (personal communication) has examined a specimen of *P. anxia* from California and has reports of *P. anxia* in Arizona.

Males of ten other *Phyllophaga* species were also captured in numbers >1000. These include *P. futilis*, *P. congrua*, *P. crassissima*, *P.*

praetermissa, *P. gracilis*, *P. hirtiventris*, *P. ephilida*, *P. rubiginosa*, *P. rugosa*, and *P. fusca*. Males of 13 species were captured in numbers >100 but <1000 and males of 15 species were captured in numbers >10 but <100 (Tables 3a and 3b). Eighteen species of *Phyllophaga* were recorded at ≥5 locations and 8 species were recorded at ≥11 locations (Tables 4a and 4b).

Geographical distributions and range extensions

Geographical distribution maps of *Phyllophaga* species captured during this study are found in Figures 3–63, arranged alphabetically by species. Shaded areas in these figures indicate the geographical ranges conveyed by Luginbill and Painter (1953) or Woodruff and Beck (1989) [*P.* (*Phytalus*) *georgiana* and *P.* (*Phytalus*) *obsoleta* only].

Most captures of *Phyllophaga* species recorded during this study were found within the geographical species distributions reported by Luginbill and Painter (1953). There are, however, several range extensions to report. The following species were found in locations in addition to those reported by Luginbill and Painter: *P. curialis* (Figure 14), *P. drakei* (Figure 17), *P. forbesi* (Figure 20), *P. foxii* (Figure 22), *P. futilis* (Figure 25), *P. gracilis* (Figure 29), *P. gracilis* var. *angulata* (Figure 30), *P. hirtiventris* (Figure 33), *P. longispina* (Figure 40), *P. lota* (Figure 41), *P. marginalis* (Figure 43), *P.* (*fraterna*) *mississippiensis* (Figure 46), *P. postrema* (Figure 50), *P. praetermissa* (Figure 51), *P. quercus* (Figure 53), and *P. taxodii* (Figure 59). Riley (1988) had previously noted range extensions of *P. forbesi*, *P. quercus*, and *P. taxodii* into Louisiana.

Changes in population levels from year to year within sites

Numbers of beetles of a particular species changed dramatically from year to year at the same trapping location. For example, traps were maintained at the Auburn, Alabama site during the 1997, 1998, and 1999 seasons for approximately the same time period each year. The numbers of *P. gracilis* captured declined from 1123 in 1997, to 710 in 1998, and to 98 in 1999 (Tables 5, 6, 7). In Lexington, Kentucky, from 1999 to 2000, the numbers of each of the six species captured more than doubled (Tables 29, 30).

Factors affecting the size of the population include not only weather during the flight period, but soil moisture and tilth conditions suitable for oviposition, egg hatch, and growth of larvae during the previous year or years that it takes for development to adults. Quality and quantity of larval host plants, soil textural characteristics, and species' preferences for soil types also factor into population size and distributions (Katovich et al. 1998). Changes in population size of other species at other trapping sites may be seen in Tables 5–97. Species captured at a particular site changed from year to year as well, indicating that multiyear studies will yield a more realistic picture of population sizes and species distributions than will a single year of captures.

Male captures with sex attractants

The most important finding of the present study was the demonstration of the extensive use of the methyl esters of L-valine and L-isoleucine as sex attractants in the mate recognition systems of the *Phyllophaga*. In 56 discrete locations across the US and Canada, during 94 observation periods (some locations were trapped for multiple years), 61 species of *Phyllophaga* were captured. The overwhelming majority (58) of these species are found in the *Phyllophaga (sensu stricto)* subgenus. Since there are 147 species in this subgenus in America north of Mexico (Evans 2003; Smith and Evans 2005), 39% of the species in this group were captured in traps during the course of this study.

Male trap captures are graphically illustrated in Figures 64–126. The figures are arranged alphabetically by *Phyllophaga* species. Within each species figure, graphs are arranged alphabetically by state or province abbreviation. The graphs demonstrate three general patterns of species-specific male responses to a particular blend or group of blends. The three general patterns are displayed in Figure 127. First, some species, such as *P. vehemens*, flew primarily to the 100/0 L-valine methyl ester/L-isoleucine methyl ester lure and were sensitive to increasing amounts of L-isoleucine methyl ester in the other blends, its presence significantly reducing captures[1]. *P. congrua*, however, had a broader response profile and was captured not only with the 100 % L-valine methyl ester lure, but also with blends containing 10%–20% L-isoleucine methyl ester (Figure 71). A similar situation was seen in responses of male *P. hirtiventris* (Figure 96). The second case (Figure 127) involved species such as

P. forbesi that were captured primarily with the 100% L-isoleucine methyl ester lure. Increasing titers of L-valine methyl ester resulted in reduced or no captures[2]. In the third case (Figure 127), some species of *Phyllophaga*, such as *P. glabricula*, required the presence of both compounds before captures occurred[3]. An examination of these male- response curves reveals that, whereas certain species had a rather broad response range to the L-valine methyl ester/L-isoleucine methyl ester blends,[4] others exhibited response curves occupying a narrower range of blends[5].

Specificity of response over time and space

A striking aspect of the intra-specific male flight responses to the sex attractants was their consistency between years and across geographic locations. Several species were recorded at only one site, but were captured at that site for two consecutive years[6]. The response profiles for each species in both years at those sites were nearly identical.

The majority of *Phyllophaga* species were recorded at more than one site (Tables 4a and 4b). As with the across-years comparison above, the intra-specific male-response curves from different geographic locations are similar as well. For instance, only five specimens of *P. balia* were captured during this study, but they were captured at three different locations (Figure 6) and all with the 100% L-isoleucine methyl ester lure (Figure 68). Nearly 7000 *P. congrua* were captured at eight different sites (Figure 9) and all sites exhibited similar response curves (Figure 71). Comparable results are seen when other species are examined[7].

Some species were captured at only one location and only during a single year, but multiple catches over time in the same or nearby blends furnish a series of independent observations that support responses to a particular lure despite the small numbers. For instance, six specimens of *P. davisi* Langston were captured in Marion Junction, Alabama in 1999, all in traps baited with the 100% L-isoleucine methyl ester lure (Figure 77) on six different dates between 4/5 and 4/28. *P. davisi* is a species that Luginbill and Painter (1953) indicate is rare, with “Only a few specimens seen.”

In Auburn, AL in 1998 two specimens of *P. diffinis* (Blanchard) were captured with the 100% L-valine methyl ester lure (Figure 78) - one taken on 4/16 and one taken on 4/21.

Another uncommon species, *P.* (*Phytalus*) *georgiana* Horn, was captured in Tifton, Georgia, in 2000. Two individuals of this species flew to the 100% L-valine methyl ester lure (Figure 89), one on 7/17 and one on 7/21. Woodruff and Beck (1989) report that no adult host plants are recorded, the larva is undescribed, and the life cycle is unknown. This species is one of seven North American species in the subgenus *Phytalus*. Members of this subgenus can be discriminated from the *Phyllophaga (sensu stricto)* by their cleft tarsal claws.

P. mariana is reported as a very rare species (Luginbill and Painter 1953). Four specimens were captured in Tifton, Georgia, in 2000 and 2001, on four different dates, in traps baited with the 90/10 or 80/20 L-valine methyl ester/L-isoleucine methyl ester blends (Figure 107).

Two specimens of *P. taxodii* Langston were captured in Louisiana in 1997 in the 35/65 L-valine methyl ester/L-isoleucine methyl ester blend (Figure 122), one on 7/3 and the other on 8/15. Luginbill and Painter (1953) list this species as uncommon, having been captured only in AL and MS. However, Riley (1988) reports that this species is not frequently taken at lights and that fair numbers have been captured in flight-intercept traps 50 feet above the ground in cypress stands. Riley concludes that a lack of light trap catches gives the impression of rarity but that the method of collection may be more important.

Similarly, R. J. Bauernfiend in Manhattan, Kansas indicated that in many years of light trapping he had never captured *P. sylvatica*, and was surprised to capture 104 individuals of this species during two years of sex attractant trapping (Figure 121).

Of some interest is the capture of both *P.gracilis* and *P.gracilis* variety *angulata* in traps baited with 100% L-isoleucine methyl ester (Figures 92 and 93). Woodruff and Beck (1989) indicate that “The exact status of this form (*angulata*) awaits further study”. The different forms of the male genitalia easily separate these populations of *P. gracilis*. Photos of the two genitalic forms can be seen in Luginbill and Painter (1953). The two forms are sympatric over a large range (Figures 29 and 30). Langston (1927) provides illustrations of the genitalia indicating what appears to be a form intermediate between *P. gracilis* and *P. gracilis* variety *angulata*.

Intra-location species interactions

The location tables (Tables 5–97) list the blends presented at each site in a particular trapping year and the numbers of *Phyllophaga* captured with each blend. At each site, the listed species are, by definition, sympatric. At some sites, sympatric species displayed asynchronous flight patterns, including species captured days, weeks, or in some cases, months apart. At other sites, different species of *Phyllophaga* were synchronic as well as sympatric, but may or may not have been captured with the same sex attractant blends. The distinction of whether males of different species were or were not captured in the same blends is important because it can aid in identifying locations where inter-specific competition for pheromonal space may be occurring. Congeneric males flying to the same sex attractant blends indicate situations where there is potential for inter-specific mating interactions that afford opportunities for investigation into reproductive isolation involving additional species-specific sex attractant compounds, close-range mating behavior, and/or mating at different times.

Each of the three scenarios (1. sympatric and synchronically flying species captured using different blends; 2. sympatric and asynchronically flying species captured using the same blend; 3. sympatric and synchronically flying species captured using the same blend) were encountered in the course of this study, individually as well as in combination at different study sites. The following examples illustrate the three scenarios.

- In Lexington, Kentucky, in 1999, both *P. futilis* and *P. rugosa* flew synchronically between 5/10 and 7/7, but were captured in traps baited with different blends of L-valine methyl ester/L-isoleucine methyl ester (Figure 128).

- In Lincoln, Nebraska, in 1999, both *P. vehemens* and *P. crenulata* were captured in the trap baited with the 100% L-valine methyl ester, but their flight periods were separated by 18 days during which no males of either species were captured. *P. vehemens* flew from 5/16 through 5/25, whereas *P. crenulata* flew from 6/12 through 7/5 (Figure 129).

- In Amherst, Massachusetts, in 1999, both *P. anxia* and *P. longispina* flew to the 100% L-isoleucine methyl ester lure during the period between 5/18 and 6/15 (Figure 130). This latter scenario is the most engaging because it is in this case that the potential for conflict in terms of pheromonal space arises.

From the male capture data at the various trapping sites, many examples of different species flying synchronically, sympatrically, and to the same blends or blend groupings have been documented. However, nothing is known about whether these species fly at different times of the night or how close-range courtship behaviors are involved in mate recognition. Figures 131–133 display detailed information relating male response specificity curves and time of flight from three sites that demonstrate the complexity of interactions that can occur over a season. Figure 131 (KS Manhattan #2, 2001), demonstrates that *P. inversa* and *P. vehemens* flew synchronically to the 100% L-valine methyl ester lure. Similarly, there is potential for interaction between *P. rubiginosa* and *P. sylvatica* (middle L-valine methyl ester/L-isoleucine methyl ester blends), *P. crassissima* and *P. fusca* (lower L-valine methyl ester/L-isoleucine methyl ester blends), and *P. futilis* and *P. bipartitia* (100% L-isoleucine methyl ester lure). In the July and August flights at the same site, *P. glabricula*, *P. affabilis*, and *P. ephilida* were captured synchronically, but with different blends. Figure 132 (KY Lexington, 2000) shows that *P. futilis* and *P. hirticula* flew synchronically to the 100% L-isoleucine methyl ester lure, whereas *P. ephilida* was captured with the same lure, but later in the season. In Figure 133 (MA Amherst, 1999), synchronic species *P. forsteri*, *P. fraterna*, and *P. fusca* displayed overlapping male response curves to L-valine methyl ester/L-isoleucine methyl ester mixes, whereas *P. anxia*, *P. longispina*, and *P. drakei* also flew synchronically to the 100% L-isoleucine methyl ester lure.

Table 98 outlines, in a briefer format, other trapping locations and the species involved where inter-specific attraction might occur as a result of competition for pheromonal space. However, the possibility of interactions postulated by the overlap of the male response curves in time and space may not necessarily reflect the reality in the field in that females may or may not have a narrower range of sex pheromone blend production than is suggested by what the males are capable of responding to. The potential for inter-specific interactions might be predicted with greater accuracy by combining analysis of blend ratios produced by a number of individual females with knowledge of male captures by various blends and determining if male response curves overlap congeneric female production curves.

Interspecific copulation between *Phyllophaga* species has been reported in the literature. Fattig (1944) reports (p. 26) that he collected a male *P. hirticula* copulating with a female *P. anxia*. Referencing the data from the present study, *P. hirticula* males were captured in traps baited with the 100% L-isoleucine methyl ester lure (Figure 95). *P. anxia* males of both the northern and the southern genitalic form were also captured in traps baited with the 100% L-isoleucine methyl ester lure (Figures 66a, 66b, 66c, 66d, 66e and 67). It is likely that the male *P. hirticula* flew upwind following an L-isoleucine methyl ester plume to find not a conspecific female *P. hirticula*, but a congeneric female *P. anxia*. *P. hirticula* and *P. anxia* males possess genitalia whose cuticular structures are exceedingly different (see images in Woodruff and Beck, 1989). Their soft sac structures are very different as well (P.S. Robbins, personal observation). Their vestitures also differ, *P. anxia* being glabrous and *P. hirticula* being hirsute. Although interspecific genitalic differences could and sometimes do play a role in reproductive isolation of some taxa (Eberhard 1985, Sota and Kubota 1998), genitalic differences clearly did not prevent copulation from taking place in this case.

Copulation does not inevitably lead to fertilization or production of offspring (Eberhard 1996), and similarly, attraction to a congeneric *Phyllophaga* female does not inevitably lead to copulation. In a study from Costa Rica, Eberhard (1993), reporting on the copulatory behavior of several species of *Phyllophaga*, states of *P. vicina*, that "Early in the evening solitary females rested immobile and apparently emitted an attractant, as males arrived in flight from downwind. The pheromone apparently also attracted males of *P. valeriana*, as on three occasions I saw one or more males of this species hover near a female *P. vicina* (beetles were captured to verify their species identity). One *P. valeriana* male landed on the female, then immediately took flight and left, suggesting that a second cue, possibly on the beetle's surface, was used to distinguish species identity. Contact pheromones may be used in the melolonthine genus *Macrodactylus* (Eberhard 1992)." These observations indicate that more studies are needed to clarify the role of morphology and/or contact pheromones in close-range mate recognition in *Phyllophaga*. Eberhard (1993) reports that "secondary sexual modifications of the sculpturing of the front legs, the ventral bristles, and the overall leg length of male *Macrodactylus* may function as courtship devices prior to and during copulation". Although the *Phyllophaga* are renowned for their extravagant and often asymmetric genitalic morphology, male hind tibial spurs also often assume unique configurations that provide excellent taxonomic characters for species assignments (Luginbill and Painter 1953; Woodruff and Beck 1989; Woodruff and Sanderson 2004). The role tibial spurs play in close-range mate recognition or copulatory courtship in the *Phyllophaga* is unclear. Males of some *Phyllophaga* species also have extensive ventral bristles or possess unique morphological characters on the venter, similar to *Macrodactylus* (P.S. Robbins, personal observation).

Intraspecific variation in male response: *P. anxia*

The consistency of intra-specific male responses over space and time that was discussed earlier contrasts with the extensive variation noted in the male-response curves of *P. anxia* to the various blends of L-valine methyl ester/L-isoleucine methyl ester sex attractants (Figures 66a, 66b, 66c, 66d, and 66e). The variations demonstrated in the male-response profiles of *P. anxia* are of four general forms:

- Those profiles from locations where the males flew primarily to L-valine methyl ester alone (Figure 134 and Figures 66a, 66b, 66c, 66d, and 66e including CT Vernon, 1999; NY Bellona, 1999 and 2000; NY Saratoga Springs, 1999 and 2000; NY Warwick, 1999 and 2000; NY Waterloo #1, 1998 NY Waterloo #1, 1999 and 2000; NY Waterloo #2, 1998; ON Woodlawn, 1999 and 2000; PA State College, 1999 and 2000, WI Babcock, 1999 and 2000)

- Those profiles from locations where the males primarily flew to L-isoleucine methyl ester alone (Figure 135 and Figures 66a, 66b, 66c, 66d, and 66e including MA Amherst, 1999 and 2000; NH Madbury, 1999 and 2000).

- Those profiles from locations where males flew to L-valine methyl ester alone or L-isoleucine methyl ester alone on the same night in the same place (Figure 136 and Figures 66a, 66b, 66c, 66d, and 66e, ME Lincolnville Center, 1999 and 2000; NY Franklinville, 1999; VT Burlington, 1999 and 2000).

- Those profiles from locations where the males were mainly captured in traps baited with blends of L-valine methyl ester and L-isoleucine methyl ester (Figure 137 and Figures 66a, 66b, 66c, 66d, and 66e, MA Carver, 1996, 1998, 1999, and 2000; MA Lakeville, 1999 and 2000; MA Plympton #1, 1996; MA Plympton #2, 1996; RI Kingston, 1999 and 2000).

All the *P. anxia* males from Figures 134 to 137, as well as all other *P. anxia* males in Figures 66a, 66b, 66c, 66d, and 66e are of the northern genitalic form (Luginbill and Painter 1953; Woodruff and Beck 1989). Male *P. anxia* of the southern genitalic form (Luginbill and Painter 1953; Woodruff and Beck 1989) were captured exclusively with L-isoleucine methyl ester alone (Figure 67). They were captured in both a smaller number of locations (8 vs.25) and in much smaller numbers (20 vs. 20,640) (Table 2a) than *P. anxia* males of the northern genitalic form. Unpublished data from studies conducted at the Franklinville, NY, site suggest that L-isoleucine methyl ester responding *P. anxia* males (both northern and southern genitalic forms) are more sensitive to the presence of L-valine methyl ester than are L-valine methyl ester responding males to the presence of L-isoleucine methyl ester. Male captures in the L-isoleucine methyl ester-baited traps may have been suppressed by the presence of the L-valine methyl ester at the trap sites.

The manner in which the different forms of the *P. anxia* male sex pheromone response profiles are distributed across North America reveals important information. The five locations yielding response profiles (10 site-years) from *P. anxia* males that were captured in blends of both L-valine methyl ester and L-isoleucine methyl ester are found only in southeast Massachusetts and Rhode Island (see Figures 66a, 66b, 66c, 66d, and 66e including all the MA Carver, MA Lakeville, MA Plympton #1, MA Plympton #2 and RI Kingston sites). Surrounding these five locations are trapping sites to the west (as far west as Wisconsin) and to the north (as far north as the provinces of Nova Scotia and Ontario) that represent those populations of *P. anxia* males that responded to only L-valine methyl ester or to only L-isoleucine methyl ester, but did not require a blend of the two for capture (Figure 138). The male response curves generated by the beetle captures at those trapping sites yield a distribution map that is patchy in terms of unequal distributions of the two populations. Some sites harbor only one of the two populations, while other sites hold both, thus generating a bimodal distribution curve.

A detailed examination (including the soft sacs) of male individuals of the L-valine methyl ester responding populations, the L-isoleucine methyl ester responding populations, and the blend responding populations of *P. anxia* revealed no character that could be used to differentiate the populations. Further work is planned that will use DNA sequence data from both mitochondrial and nuclear genes to generate gene genealogies with which to document genetic relationships within and among the three races across the US. Microsatellite markers will also be used to characterize allele frequencies in natural populations and consequently estimate the extent of gene exchange among different pheromone races where they occur together and between geographically isolated populations of single pheromone races.

Intra-specific variation in male response: *P. fraterna*

A second instance of intra-specific variation in male response to blends presented was noted at the State College, Pennsylvania, trapping site in 1999 and 2000. Male individuals of a species determined as *P. fraterna* were captured by two blend groupings in both years (Tables 80 and 81 and Figures 85 a, 85b, and 86). In 1999, 18 males were captured with the 0/100 L-valine methyl ester/L-isoleucine methyl ester blend, whereas 13 males were captured with the L-valine methyl ester/L-isoleucine methyl ester mixtures. In 2000, 19 males were captured with the 0/100 L-valine methyl ester/L-isoleucine methyl ester blend whereas 5 males were captured with the L-valine methyl ester/L-isoleucine methyl ester mixtures. *Phyllophaga fraterna* from locations other than Pennsylvania were captured exclusively in the blends of L-valine methyl ester/L-isoleucine methyl ester (Figures 85a and 85b).

Summary and Conclusions

This study demonstrates the extensive use of the methyl esters of L-valine and L-isoleucine in the mate recognition systems of a widely distributed and speciose taxon. Since each trapping site is a snapshot of activity over a very restricted area, it is compelling that nearly 40% of the *Phyllophaga* (*sensu stricto*) species in America north of Mexico were captured, despite all the possible locations that were not trapped.

Consistency in male response among geographically separated populations of conspecifics was demonstrated in numerous examples. This was useful to document in itself because it provided information concerning sex attractant use in a taxon that had never before been investigated in this fashion. However, this information also served, perhaps more importantly, to contrast and highlight the unusual geographic variation in male response to sex attractants between various populations of *P. anxia* and in a more minor way, *P. fraterna*.

This study also documents the interspecific interactions between *Phyllophaga* species, through both literature citations and capture results. These interactions may be as benign as attraction to congeneric females (Eberhard 1993), with presumably little or no accompanying loss of fitness, or may involve copulation and perhaps exchange of genetic material (Fattig 1944), resulting in a more expensive or even fatal conclusion. Interactions between species are of great interest because of their connection to both species concepts and hybridization studies (Arnold 1997, Claridge et al. 1997, Rand and Harrison 1989).

Since this trapping study was terminated in 2001, additional research on sex pheromones of the *Phyllophaga* has been accomplished that extends the understanding of mate finding in this large genus. This research will have bearing on the phylogenetic relationships of this group as well.

The sex pheromone of *Phyllophaga crinita* was identified as methyl 2-(methylthio)benzoate (Robbins et al. 2003). Interestingly, Coca-Abia (2002) has recently resurrected the genus *Trichesthes* and removed *P. crinita* as well as a number of other species from the *Phyllophaga* (*sensu stricto*) to *Trichesthes*. Among the species moved to *Trichesthes* were *P. lenis* and *P. tristis*, two species that have also been captured in large numbers using methyl 2-(methylthio)benzoate (P.S. Robbins, unpublished data).

The sex pheromone of *Phyllophaga* (*Tostegoptera*) *lanceolata* was identified as L-leucine methyl ester (Nojima et al. 2003). *Tostegoptera* is a small sub-genus of the Phyllophaga consisting of only two species, *Phyllophaga* (*Tostegoptera*) *lanceolata* and *Phyllophaga* (*Tostegoptera*) *squamipilosa*. Both species have been captured using L-leucine methyl ester and field tests have demonstrated that L-valine and L-isoleucine methyl esters function as antagonists to *Phyllophaga* (*Tostegoptera*) *lanceolata* males.

Notes

[1] see Figure 99, *P. inversa*; Figure 102, *P. latifrons*; Figure 106, *P. marginalis*; Figure 126, *P. vehemens*

[2] see Figure 68, *P. balia*; Figure 69, *P. bipartita*; Figure 74, *P. crenulata*; Figures 79a and 79b, *P. drakei*; Figure 82, *P. forbesi*; Figures 88a, 88b, 88c, and 88d, *P. futilis*; Figure 92, *P. gracilis*; Figure 94, *P. hirsuta*; Figure 95, *P. hirticula*; Figure 103, *P. longispina*; Figure 113, *P. postrema*; Figure 124, *P. ulkei*

[3] see Figure 64, *P. aemula*; Figure 65, *P. affabilis*; Figure 72, *P. corrosa*; Figures 73a and 73b, *P. crassissima*; Figures 83a, 83b, and 83c, *P. forsteri*; Figures 85a and 85b, *P. fraterna*; Figures 87a, 87b, 87c, and 87d, *P. fusca*; Figure 90, *P. glaberrima*; Figure 91, *P. glabricula*; Figure 104, *P. lota*; Figure 107, *P. mariana*; Figure 108, *P. micans*; Figure 112, *P. perlonga*; Figure 114, *P. praetermissa*; Figure 116, *P. quercus*; Figure 117, *P. rubiginosa*; Figures 118a and 118b, *P. rugosa*; Figure 121, *P. sylvatica*; Figure 123, *P. torta*; Figure 125, *P. uniformis*

[4] see Figures 73a and 73b, *P. crassissima*; Figures 87a, 87b, 87c, and 87d, *P. fusca*; Figure 117, *P. rubiginosa*

[5] see Figure 64, *P. aemula*; Figure 65, *P. affabilis*; Figures 83a, 83b, and 83c, *P. forsteri*; Figures 85a and 85b, *P. fraterna*; Figures 118a and 118b, *P. rugosa*; Figure 125, *P. uniformis*

[6] see Figure 64, *P. aemula*; Figure 65, *P. affabilis*; Figure 69, *P. bipartita*; Figure 72, *P. corrosa*; Figure 91, *P. glabricula*; Figure 107, *P. mariana*; and Figure 125, *P. uniformis*

[7] see Figures 11, 73a and 73b, *P. crassissima*; Figures 12 and 74, *P. crenulata*; Figures 17, 79a and 79b, *P. drakei*; Figures 20 and 82, *P. forbesi*; Figures 21, 83a, 83b, and 83c, *P. forsteri*; Figures 23, 85a and 85b, *P. fraterna*; Figures 24, 87a, 87b, 87c, and 87d, *P. fusca*; Figures 25, 88a, 88b, 88c, and 88d, *P. futilis*; Figures 27 and 90, *P. glaberrima*; Figures 29 and 92, *P. gracilis*; Figures 31 and 94, *P. hirsuta*; Figures 32 and 95, *P. hirticula*; Figures 33 and 96, *P. hirtiventris*; Figures 36 and 99, *P. inversa*; Figures 40 and 103, *P. longispina*; Figures 41 and 104, *P. lota*; Figures 43 and 106, *P. marginalis*; Figures 45 and 108, *P. micans*; Figures 47 and 110, *P. nitida*; Figures 49 and 112, *P. perlonga*; Figures 50 and 113, *P. postrema*; Figures 51 and 114, *P. praetermissa*; Figures 53 and 116, *P. quercus*; Figures 54 and 117, *P. rubiginosa*; Figures 55, 118a and 118b, *P. rugosa*; Figures 58 and 121, *P. sylvatica*; Figures 60 and 123, *P. torta*; Figures 61 and 124, *P. ulkei*; and Figures 63 and 126, *P. vehemens*

Acknowledgements

This study would not have been accomplished without the participation of my co-authors. I am deeply grateful for their persistence and attention to detail. Donna Boyce, Joe Ogrodnick, and Rob Way of Communication Services here at the New York State Agricultural Experiment Station in Geneva provided the artistic guidance and technical input to produce the excellent figures seen in this publication. Thanks go to Nancy Consolie, my lab partner in the Villani soil insect lab at Cornell University for more than 13 years. Her research suggestions and invariable good humor added to this project. Marta Luisa del Campo, Anuar Morales, and Rebecca Smyth of Cornell University and Miguel Ángel Morón of the Instituto de Ecologia in Xalapa, Mexico, all contributed to making the Spanish abstract clear and understandable. My dissertation committee at Cornell University, consisting of Drs. Cole Gilbert, Rick Harrison, Charlie Linn, Wendell Roelofs, and Mike Villani, were patient and encouraging during this long study. A special note of thanks to Mike Villani who did not live to see this work published. Thanks, Mike, for encouraging me to follow the muses.

References

Andre F. 1937. White grub devastations in Iowa nurseries. *Journal of Economic Entomology* 30: 615-618.

Arnold ML. 1997. *Natural Hybridization and Evolution*. Oxford University Press.

Bessin RT. 1999. White grub control in no-till field corn, 1998. In Saxena KN, editor. *Arthropod Management Tests*. 207. Lanham, Maryland: Entomological Society of America.

Brandenburg RL, Villani MG, editors. 1995. *Handbook of Turfgrass Insect Pests*. Lanham, Maryland: Entomological Society of America.

Claridge MF, Dawah HA, Wilson MR, editors. 1997. *Species: The Units of Diversity*. London: Chapman and Hall.

Coca-Abia MM. 2002. Reestablishment of the genus *Trichesthes* Erichson, 1847 (Coleoptera: Scarabaeidae, Melolonthinae) based on phylogeny. *Journal of the New York Entomological Society* 110: 95-114.

Dunn JB, Averill AL. 1996. Survey of soil scarab insects in Massachusetts. *Cranberries* 60: 9-12.
22–23.

Eberhard WG. 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press.

Eberhard WG. 1992. Species isolation, genital mechanics, and the evolution of species-specific genitalia in three species of *Macrodactylus* beetles (Coleoptera, Scarabaeidae, Melolonthinae). *Evolution* 46: 1774-1783.

Eberhard WG. 1993. Copulatory courtship and morphology of genitalic coupling in seven *Phyllophaga* species (Coleoptera: Melolonthidae). *Journal of Natural History* 27: 683-717.

Eberhard WG. 1993. Functional significance of some secondary sexual characters in three species of *Macrodactylus* (Coleoptera: Melolonthidae). *Coleopterists Bulletin* 47: 53-60.

Eberhard WG. 1996. *Female control: sexual selection by cryptic female choice*. Princeton University Press.

Eck P. 1990. *The American Cranberry*. Rutgers University Press.

Evans AV. 2003. A checklist of the New World chafers (Coleoptera: Scarabaeidae: Melolonthinae). *Zootaxa* 211: 1-458.

Fattig PW. 1944. The *Phyllophaga* or May beetles of Georgia. Atlanta, GA: Emory University.

Francke W, Dettner K. 2005. Chemical signalling in beetles. In Schulz S, editor. *Topics In Current Chemistry*. 85–166. Berlin: Springer-Verlag.

Franklin HJ. 1950. *Cranberry insects of Massachusetts. Bulletin 445. Parts II-VII*. Massachusetts Agricultural Experiment Station.

Glover TJ, Knodel JJ, Robbins PS, Eckenrode CJ, Roelofs WL. 1991. Gene flow among three races of European corn borers (Lepidoptera: Pyralidae) in New York state. *Environmental Entomology* 20: 1356-1362.

Gordon RD, Anderson DM. 1981. The species of Scarabaeidae (Coleoptera) associated with sugarcane in south Florida. *Florida Entomologist* 64: 119-138.

Hammond A, Story RN, Murray MJ, McCown CR, Ring D. 1997. Evaluation of selected soil and foliar insecticides on sweet potatoes for control of white grubs and banded cucumber beetles, 1995. In Saxena KN, editor. *Arthropod Management Tests*. 169–170. Lanham, Maryland: Entomological Society of America.

Katovich K, Levine SJ, Young DK. 1998. Characterization and usefulness of soil-habitat preferences in identification of *Phyllophaga* (Coleoptera: Scarabaeidae) larvae. *Annals of the Entomological Society of America* 91: 288-297.

Klun JA, Cooperators . 1975. Insect sex pheromones: Intraspecific pheromonal variability of *Ostrinia nubilalis* in North America and Europe. *Environmental Entomology* 4: 891-894.

Langston J. 1927. *Phyllophaga* of Mississippi. Technical Bulletin No. 15. Mississippi Agricultural Experiment Station.

Leal WS, Matsuyama S, Kuwahara Y, Wakamura S, Hasegawa M. 1992. An amino acid derivative as the sex pheromone of a scarab beetle. *Naturwissenschaften* 79: 184-185.

Luginbill P, Painter HR. 1953. May Beetles of the United States and Canada. Technical Bulletin No. 1060. United States Department of Agriculture.

McElfresh JS, Millar JG. 2001. Geographic variation in the pheromone system of the saturniid moth *Hemileuca eglanterina*. *Ecology* 82: 3505-3518.

Nojima S, Robbins PS, Salsbury GA, Morris BD, Roelofs WL, Villani MG. 2003. L-leucine methyl ester: The female-produced sex pheromone of the scarab beetle *Phyllophaga lanceolata*. *Journal of Chemical Ecology* 29: 2439-2446.

Rand DM, Harrison RG. 1989. Ecological genetics of a mosaic hybrid zone: Mitochondrial, nuclear, and reproductive diferentiation of crickets by soil type. *Evolution* 43: 432-449.

Ratcliffe BC. 1991. *The Scarab Beetles of Nebraska*. Bulletin of the University of Nebraska State Museum.

Riley EG. 1988. The *Phyllophaga* of Louisiana (Coleoptera: Scarabaeidae). Department of Entomology, M.S. Thesis. Louisiana State University.

Robbins PS, Crocker RL, Nojima S, Morris BD, Roelofs WL, Villani MG. 2003. Methyl 2-(methylthio)benzoate: the unique sulfur-containing sex pheromone of *Phyllophaga crinita*. *Naturwissenschaften* 90: 517-520.

Roelofs WL. 1978. Threshold hypothesis for pheromone perception. *Journal of Chemical Ecology* 4: 685-699.

Saylor L. 1937. Necessary changes in status of important Rhizotrogid genera (Col. Scarabaeidae). *Revista de Entomologia* 7: 318-322.

Saylor LW. 1939. Revision of the beetles of the Melolonthine subgenus *Phytalus* of the United States. *Proceedings of the United States National Museum* 86: 157-167.

Saylor LW. 1940. Revision of the scarabaeid beetles of the Phyllophagan subgenus *Listrochelus* of the United States, with discussion of related subgenera. *Proceedings of the United States National Museum* 89: 59-130.

Smith ABT, Evans AV. 2005. A supplement to the checklist of the New World chafers (Coleoptera: Scarabaeidae: Melolonthinae) with notes on their tribal classification. *Zootaxa* 1032: 29-60.

Smith JB. 1888. Notes on some *Lachnosterna* of temperate North America, with descriptions of new species. *Proceedings of the United States National Museum* 11: 481-525.

Sota T, Kubota K. 1998. Genital lock-and-key as a selective agent against hybridization. *Evolution* 52: 1507-1513.

Vittum PJ, Villani MG, Tashiro H. 1999. *Turfgrass Insects of the United States and Canada*. 2nd Edition. Cornell University Press.

Woodruff RE. 1961. A Cuban May beetle, *Phyllophaga* (*Cnemarachis*) *bruneri*, in Miami, Florida (Coleoptera: Scarabaeidae). Gainesville: Florida Department of Agriculture and Consumer Services. Division of Plant Industry.

Woodruff RE, Beck BE. 1989. The scarab beetles of Florida (Coleoptera: Scarabaeidae) Part II. The May or June beetles (genus *Phyllophaga*). Arthropods of Florida and Neighboring Land Areas. 13. Gainesville: Florida Department of Agriculture and Consumer Services. Division of Plant Industry.

Woodruff RE, Sanderson MW. 2004. Revision of the *Phyllophaga* of Hispaniola (Scarabaeidae: Melolonthinae). *Insecta Mundi*. 18: 1–154.

Wu W, Cottrell CB, Hansson BS, Löfstedt C. 1999. Comparative study of pheromone production and response in Swedish and Zimbabwean populations of turnip moth, *Agrotis segetum*. *Journal of Chemical Ecology* 25: 177-196.

Zhang A, Robbins PS, Leal WS, Linn CE, Villani MG, Roelofs WL. 1997. Essential amino acid methyl esters: major sex pheromone components of the cranberry white grub, *Phyllophaga anxia* (Coleoptera: Scarabaeidae). *Journal of Chemical Ecology* 23: 231-245.

Figures

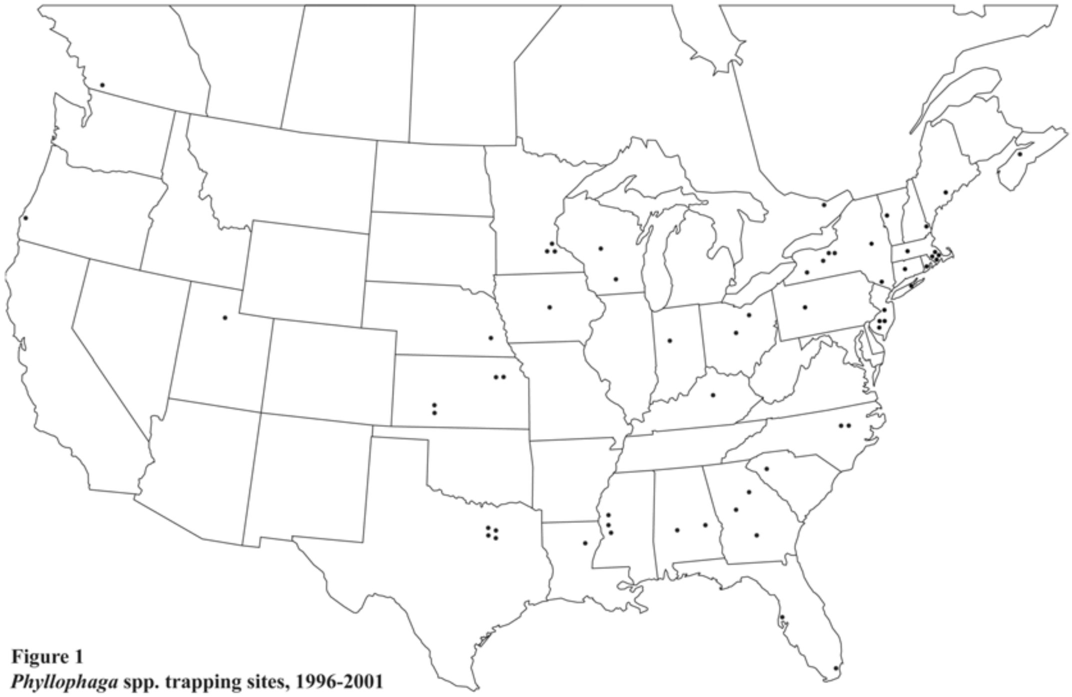


Figure 1
***Phyllophaga* spp. trapping sites, 1996-2001**

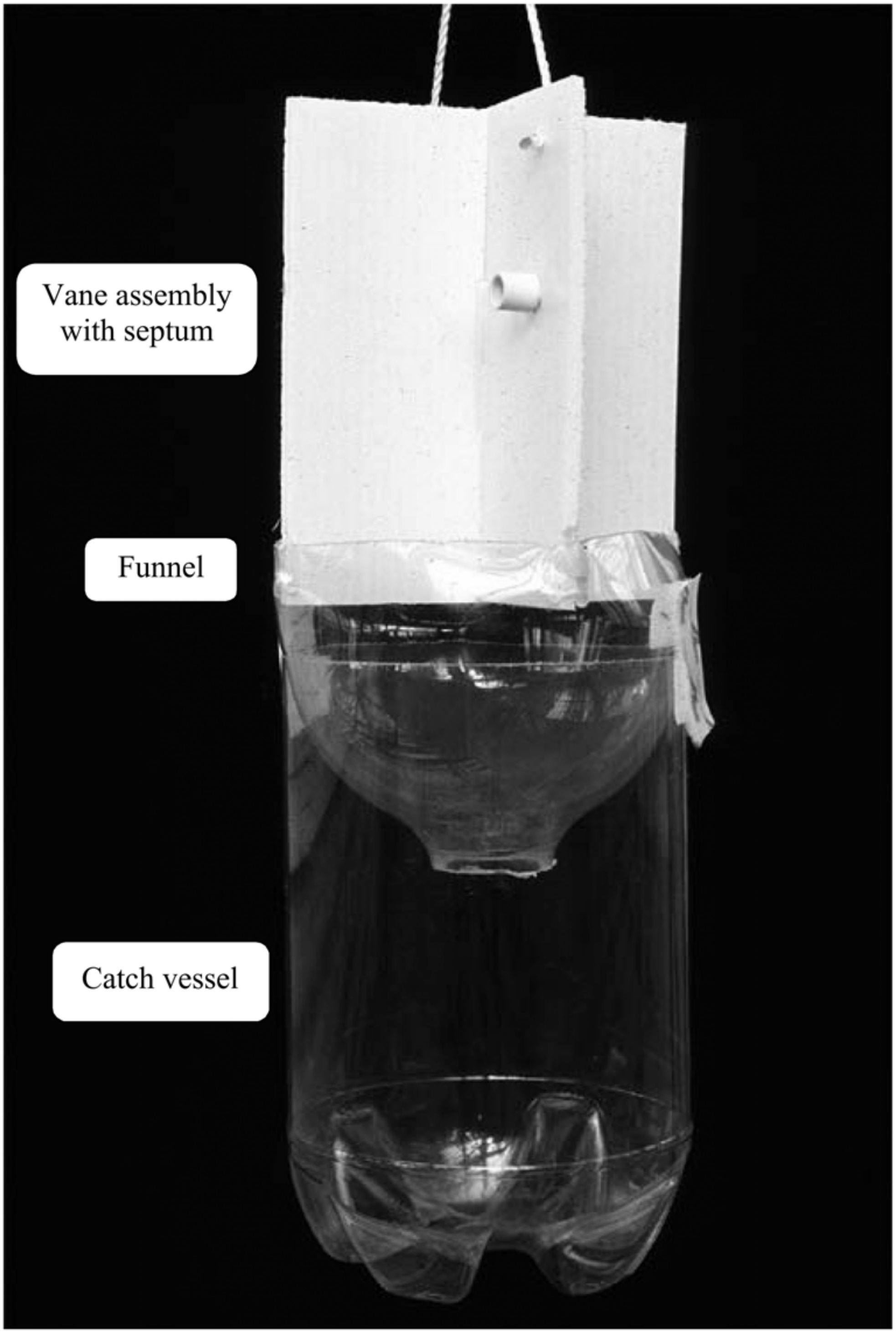


Figure 2. Cross vane trap constructed from 3 liter beverage container. Pheromones were applied to the rubber septum.

Figure 3 ***P. aemula***
• = catch sites, n = 231 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 4 ***P. affabilis***
• = catch sites, n = 77 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 5 ***P. anxia***
• = catch sites-northern form, n = 20,640 beetles
○ = catch sites-southern form, n = 20 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 6 ***P. balia***
• = catch sites, n = 5 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 7 ***P. bipartita***
• = catch sites, n = 38 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 8 ***P. clypeata***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 9 ***P. congrua***
• = catch sites, n = 6916 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 10 ***P. corrosa***
• = catch sites, n = 59 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 11 ***P. crassissima***
• = catch sites, n = 5710 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 12 ***P. crenulata***
• = catch sites, n = 15 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 13 ***P. crinita***
• = catch sites, n = 24 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 14 ***P. curialis***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 15 ***P. davisi***
• = catch sites, n = 6 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 16 ***P. diffinis***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 17 ***P. drakei***
• = catch sites, n = 91 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 18 ***P. ephilida***
• = catch sites, n = 1726 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 19 ***P. fervida***
• = catch sites, n = 3 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 20 ***P. forbesi***
• = catch sites, n = 141 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 21 ***P. forsteri***
• = catch sites, n = 141 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 22 ***P. foxii***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 23 ***P. fraterna***
• = catch sites, n = 111 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 24 ***P. fusca***
• = catch sites, n = 1040 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 25 ***P. futilis***
• = catch sites, n = 7575 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 26 ***P. (Phytalus) georgiana***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Woodruff and Beck, 1988

Figure 27 ***P. glaberrima***
• = catch sites, n = 70 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 28 ***P. glabricula***
• = catch sites, n = 274 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 29 ***P. gracilis***
• = catch sites, n = 1930 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 30 ***P. gracilis* var *angulata***
• = catch sites, n = 6 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 31 ***P. hirsuta***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 32 ***P. hirticula***
• = catch sites, n = 191 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 33 ***P. hirtiventris***
• = catch sites, n = 1820 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 34 ***P. ilicis***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 35 ***P. implicita***
• = catch sites, n = 3 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 36 ***P. inversa***
• = catch sites, n = 452 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 37 ***P. kentuckiana***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 38 ***P. lanceolata***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 39 ***P. latifrons***
• = catch sites, n = 13 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 40 ***P. longispina***
• = catch sites, n = 106 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 41 ***P. lota***
• = catch sites, n = 18 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 42 ***P. luctuosa***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 43 ***P. marginalis***
• = catch sites, n = 15 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 44 ***P. mariana***
• = catch sites, n = 4 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 45 ***P. micans***
• = catch sites, n = 172 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 46 ***P. (fraterna) mississippiensis***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 47 ***P. nitida***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 48 ***P. obsoleta***
• = catch sites, n = 22 beetles
Shaded areas = distributions from Woodruff and Beck, 1988

Figure 49 ***P. perlonga***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 50 ***P. postrema***
• = catch sites, n = 632 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 51 ***P. praetermissa***
• = catch sites, n = 2381 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 52 ***P. profunda***
• = catch sites, n = 1 beetle
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 53 ***P. quercus***
• = catch sites, n = 149 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 54 ***P. rubiginosa***
• = catch sites, n = 1594 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 55 ***P. rugosa***
• = catch sites, n = 1393 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 56 ***P. soror***
• = catch sites, n = 11 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 57 ***P. submucida***
• = catch sites, n = 5 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 58 ***P. sylvatica***
• = catch sites, n = 104 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 59 ***P. taxodii***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 60 ***P. torta***
• = catch sites, n = 4 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 61 ***P. ulkei***
• = catch sites, n = 2 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 62 ***P. uniformis***
• = catch sites, n = 872 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

Figure 63 ***P. vehemens***
• = catch sites, n = 79 beetles
Shaded areas = distributions from Luginbill and Painter, 1953

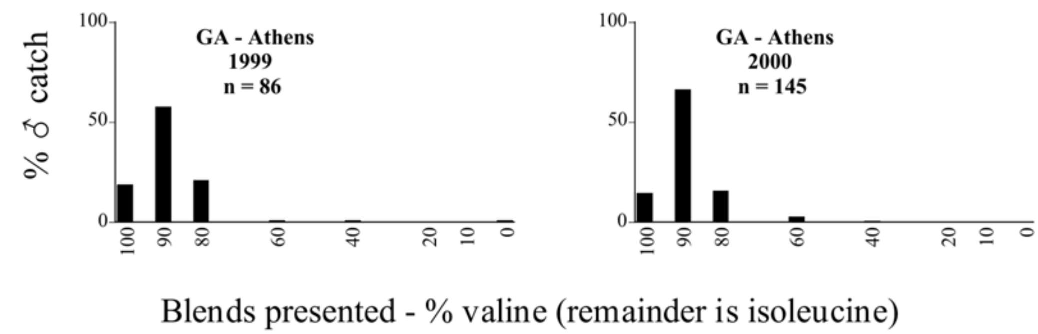


Figure 64 *P. aemula* ♂ catches

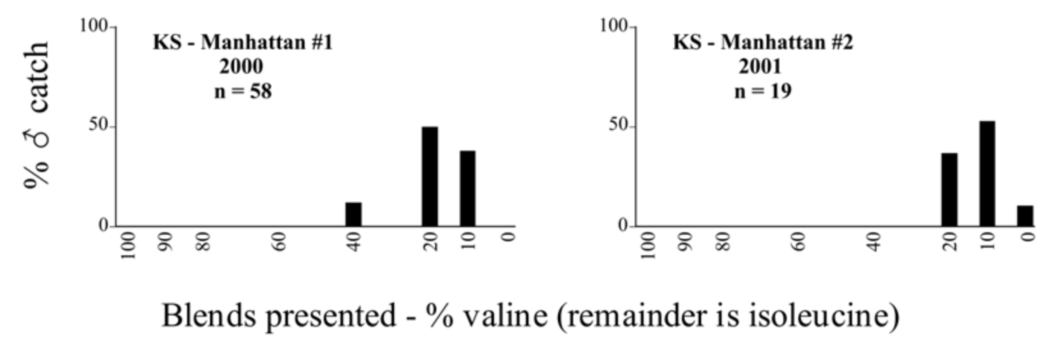


Figure 65 *P. affabilis* ♂ catches

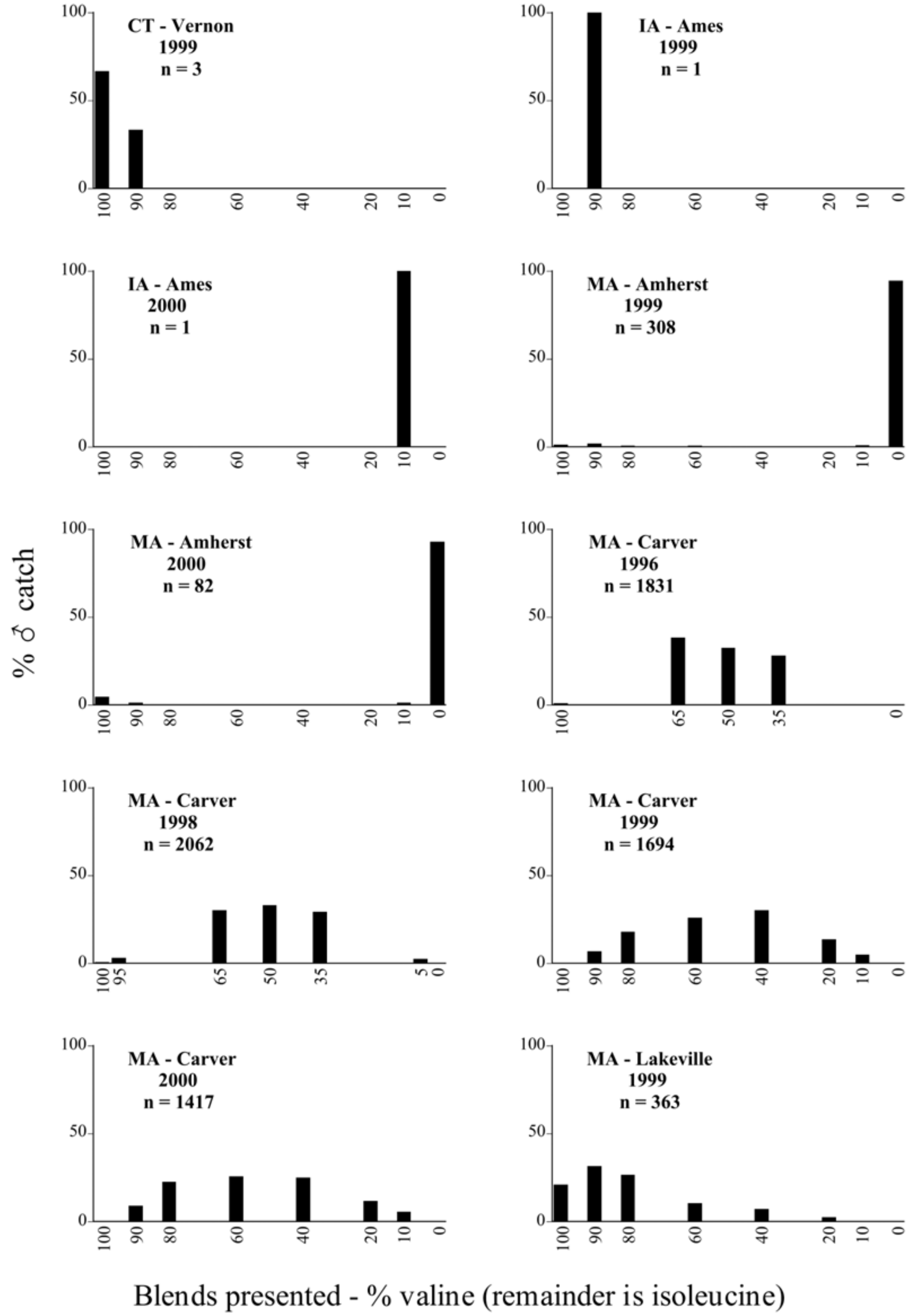


Figure 66a *P. anxia* (northern genitalic form) ♂ catches

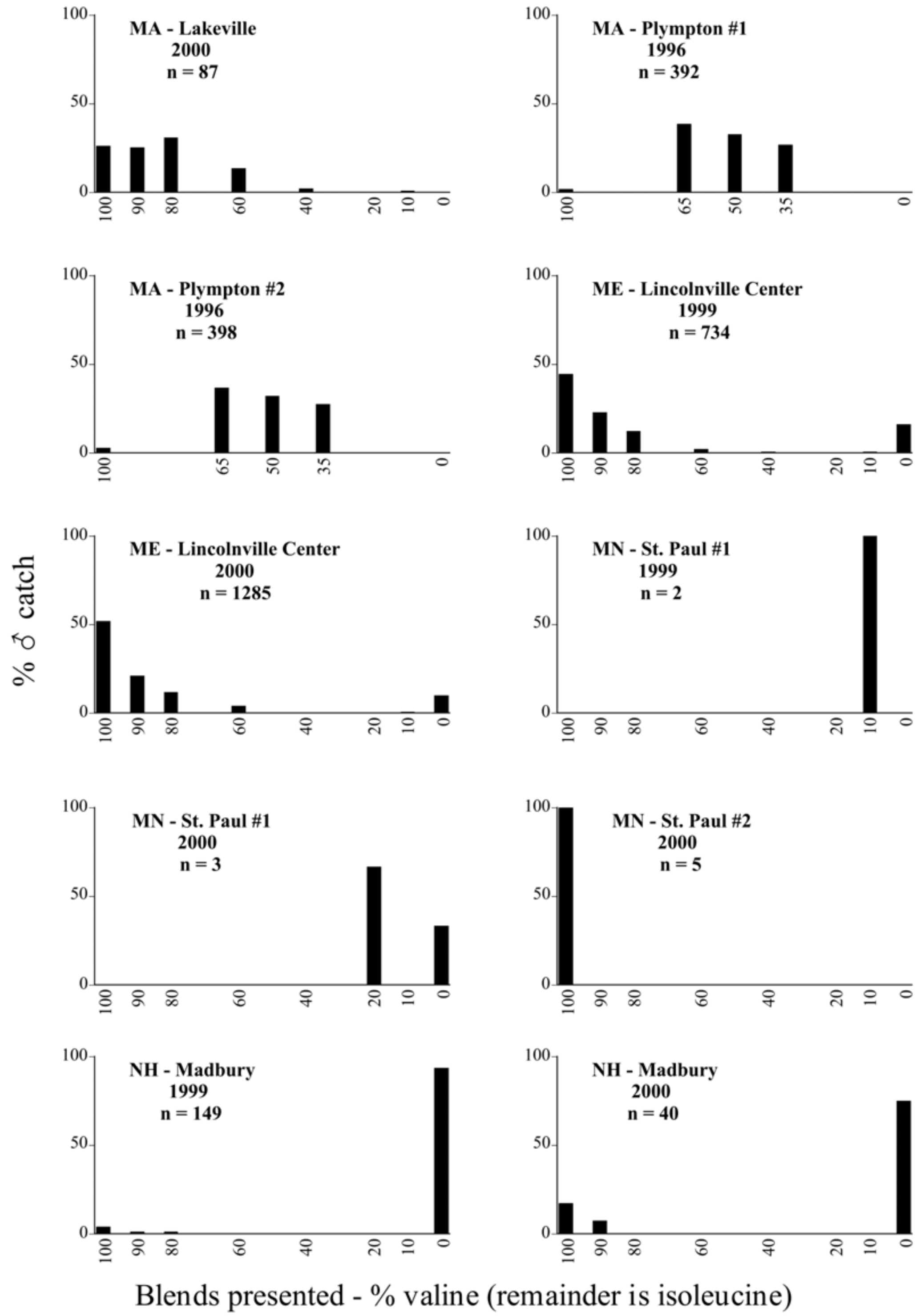


Figure 66b *P. anxia* (northern genitalic form) ♂ catches

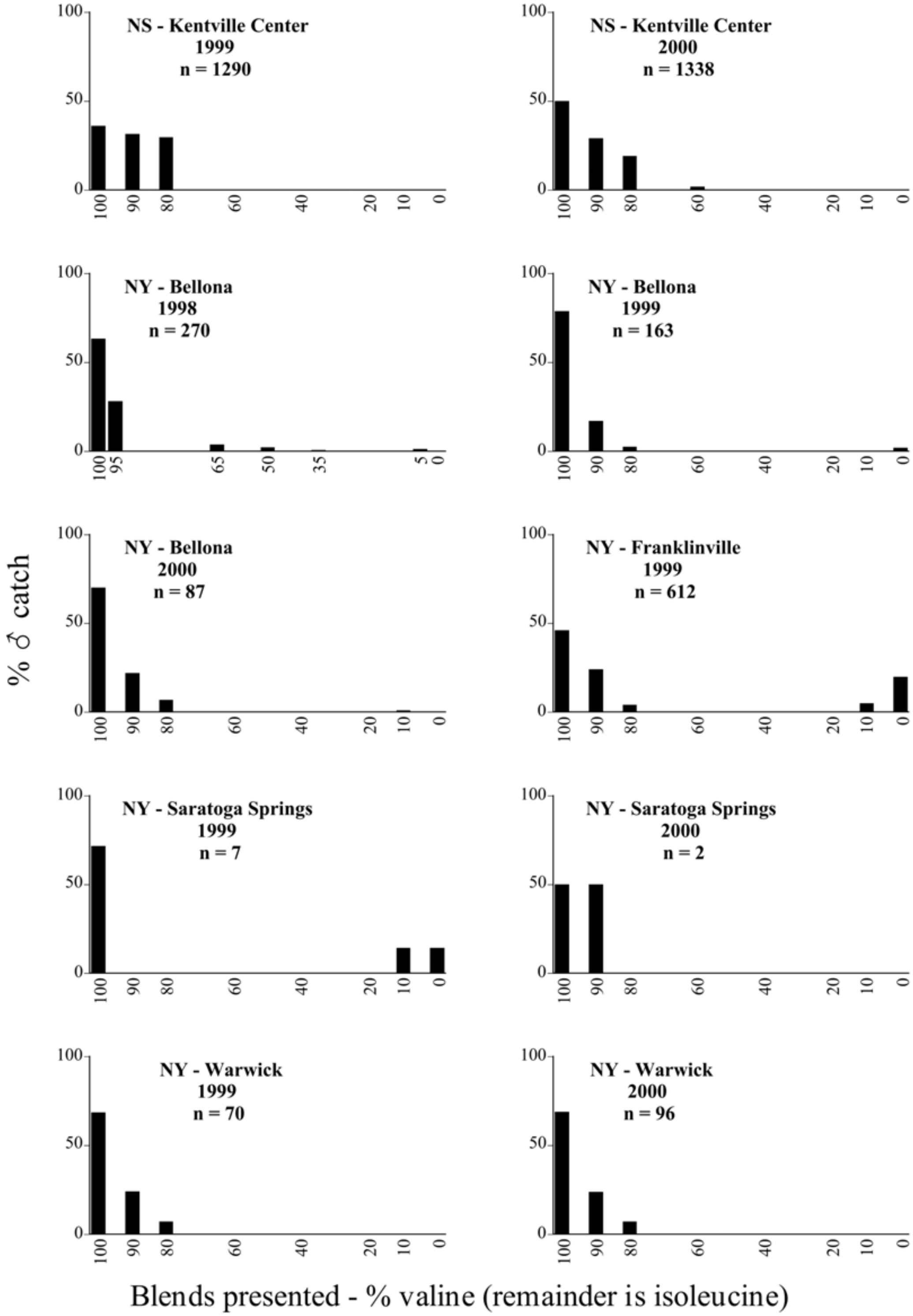


Figure 66c *P. anxia* (northern genitalic form) ♂ catches

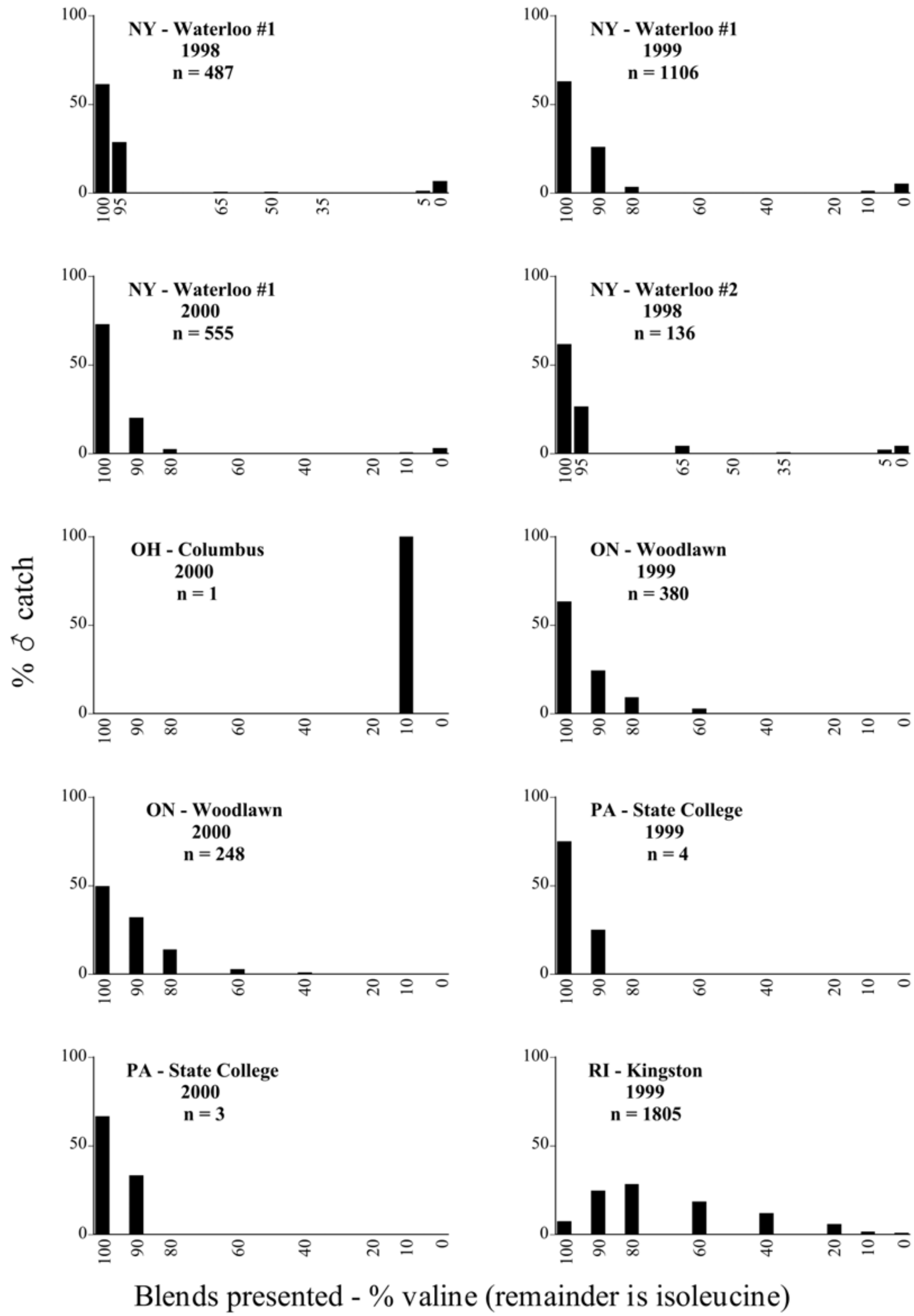


Figure 66d *P. anxia* (northern genitalic form) ♂ catches

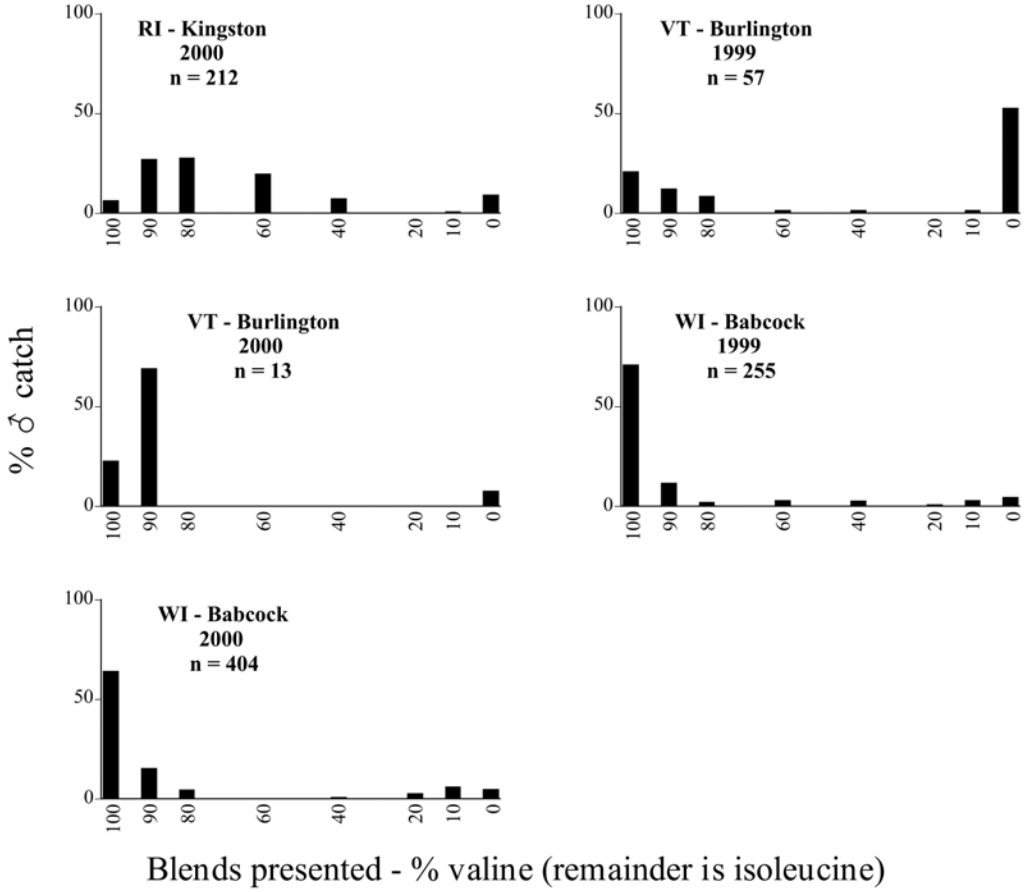


Figure 66e *P. anxia* (northern genitalic form) ♂ catches

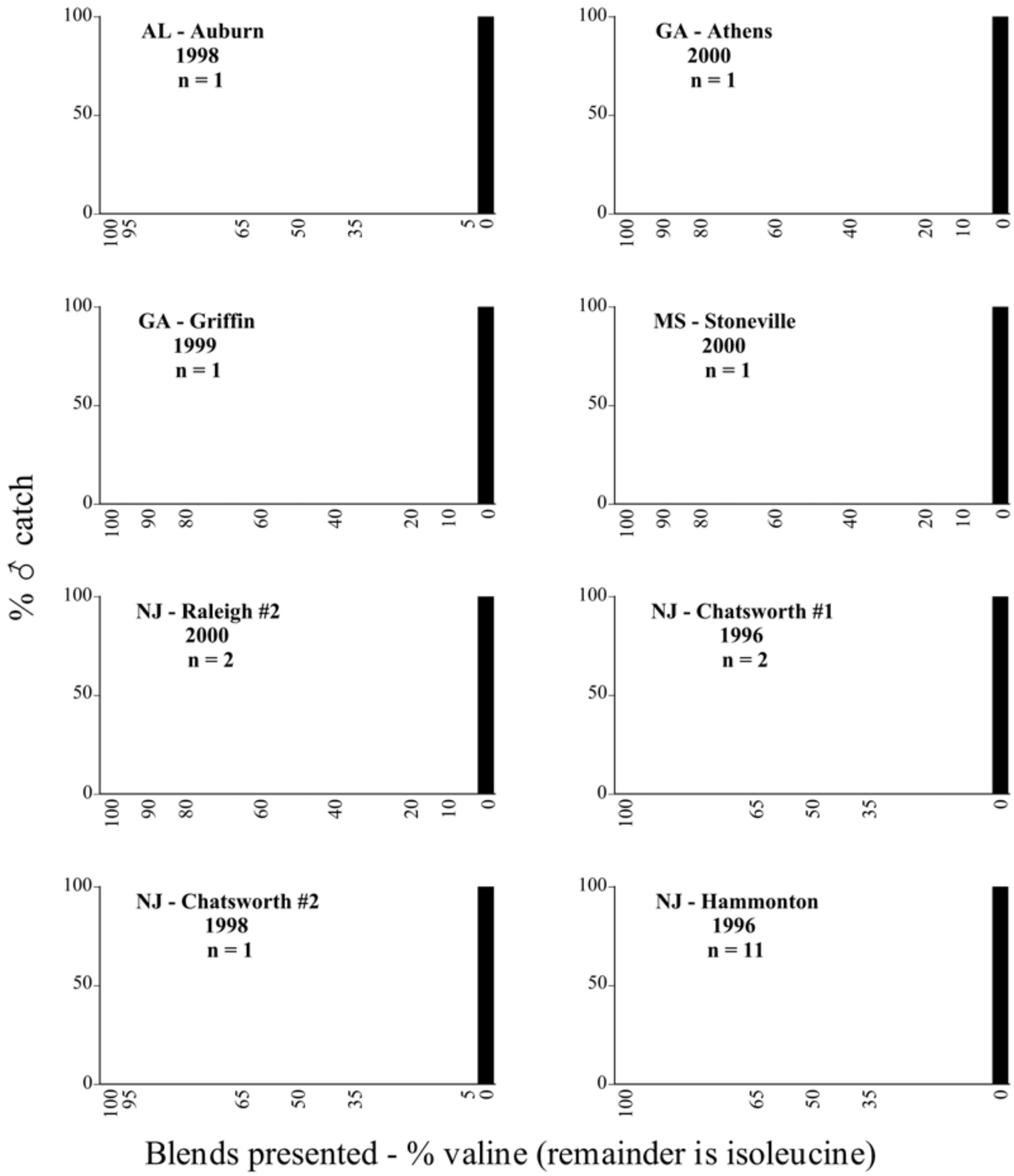


Figure 67 *P. anxia* (southern genitalic form) ♂ catches

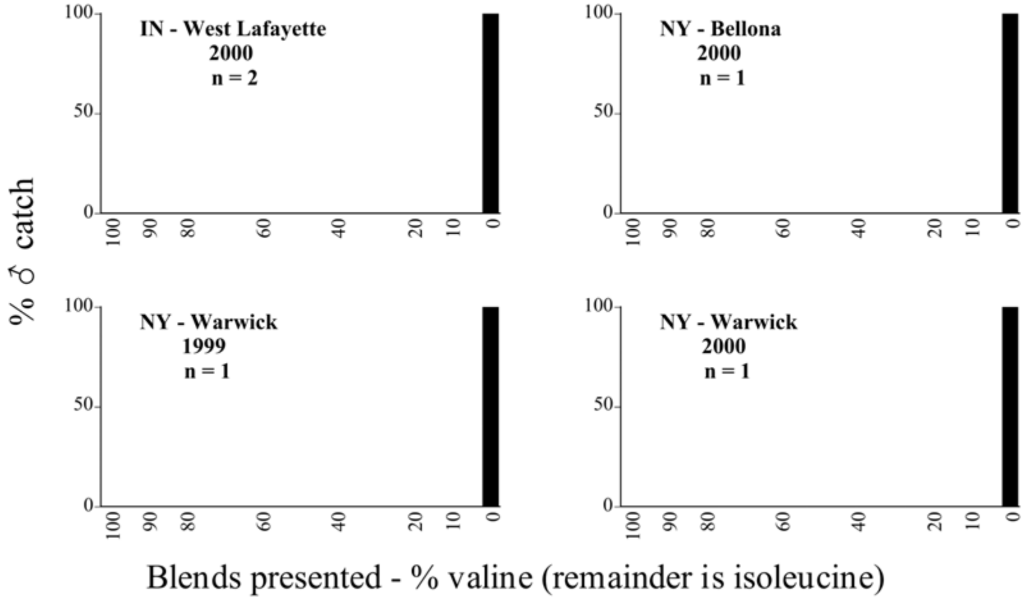


Figure 68 *P. balia* ♂ catches

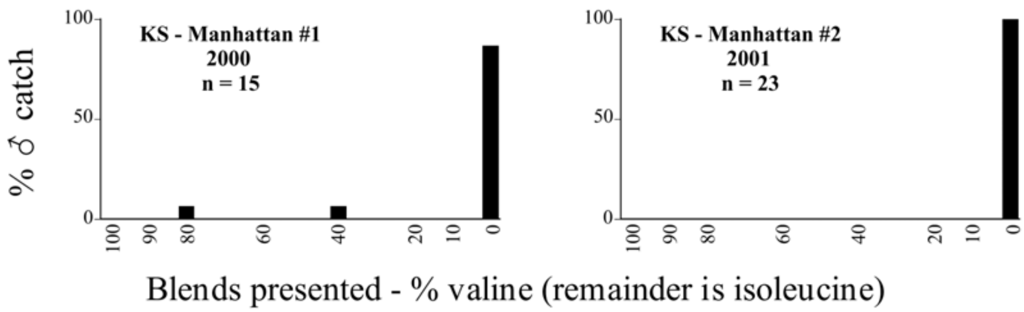


Figure 69 *P. bipartita* ♂ catches

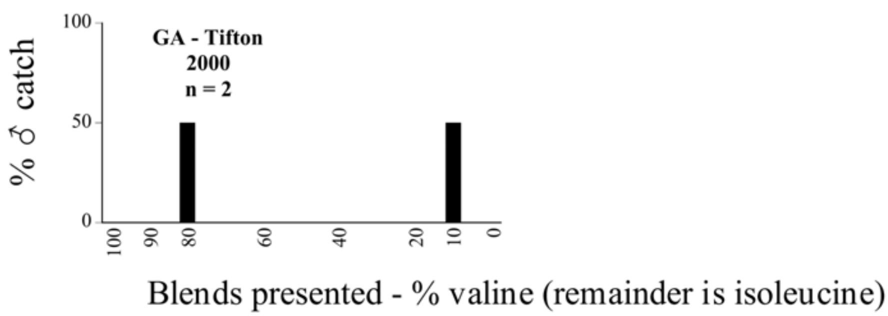


Figure 70 *P. clypeata* ♂ catches

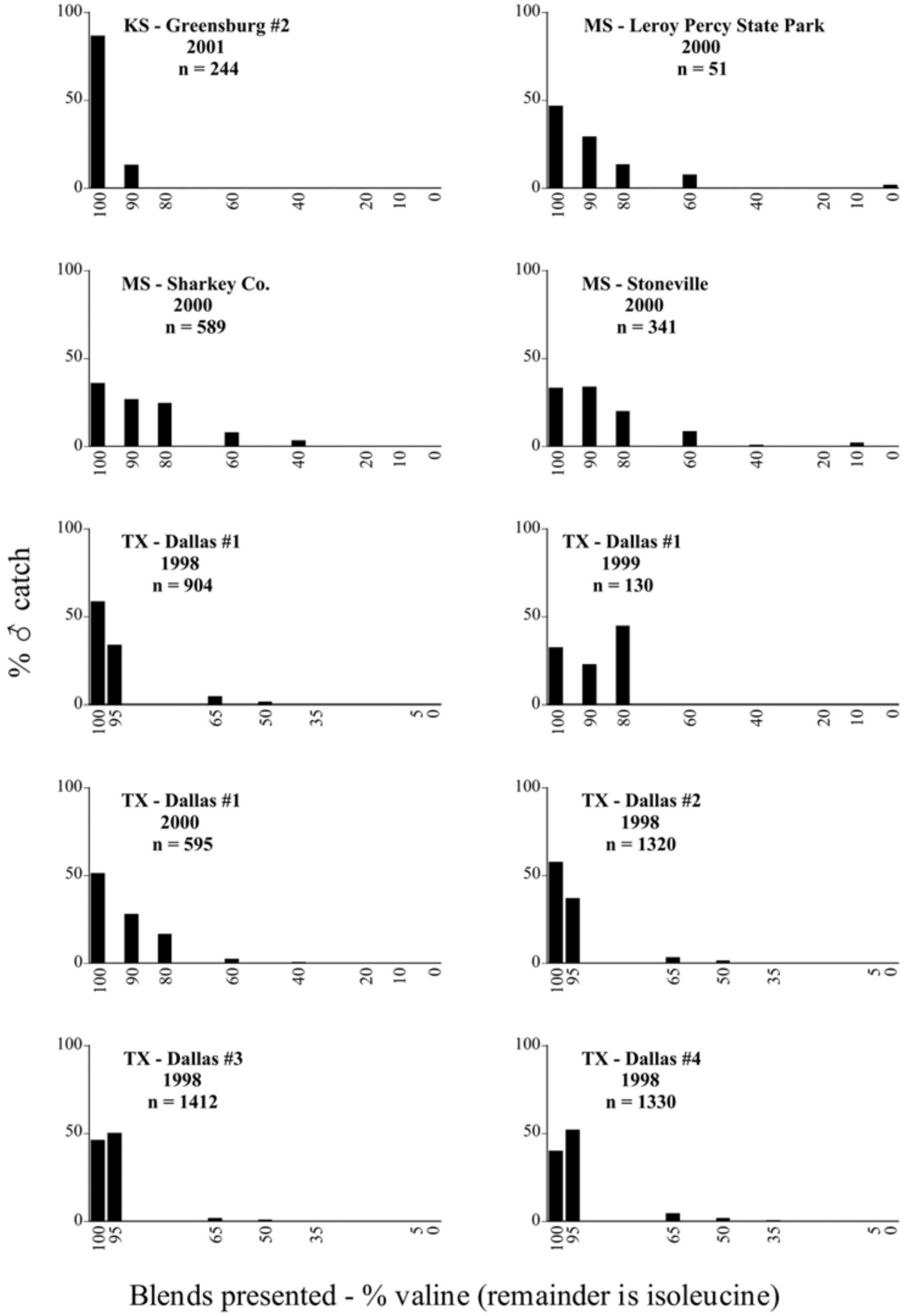


Figure 71 *P. congrua* ♂ catches

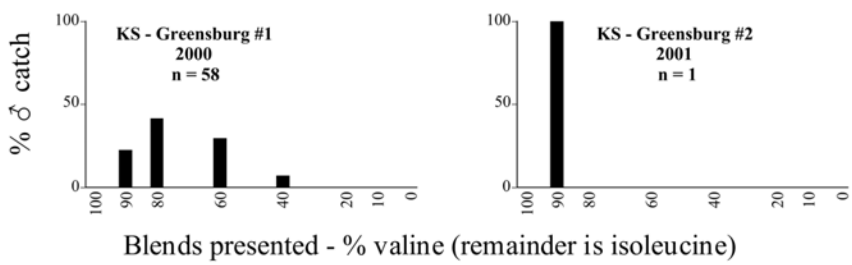


Figure 72 *P. corrosa* ♂ catches

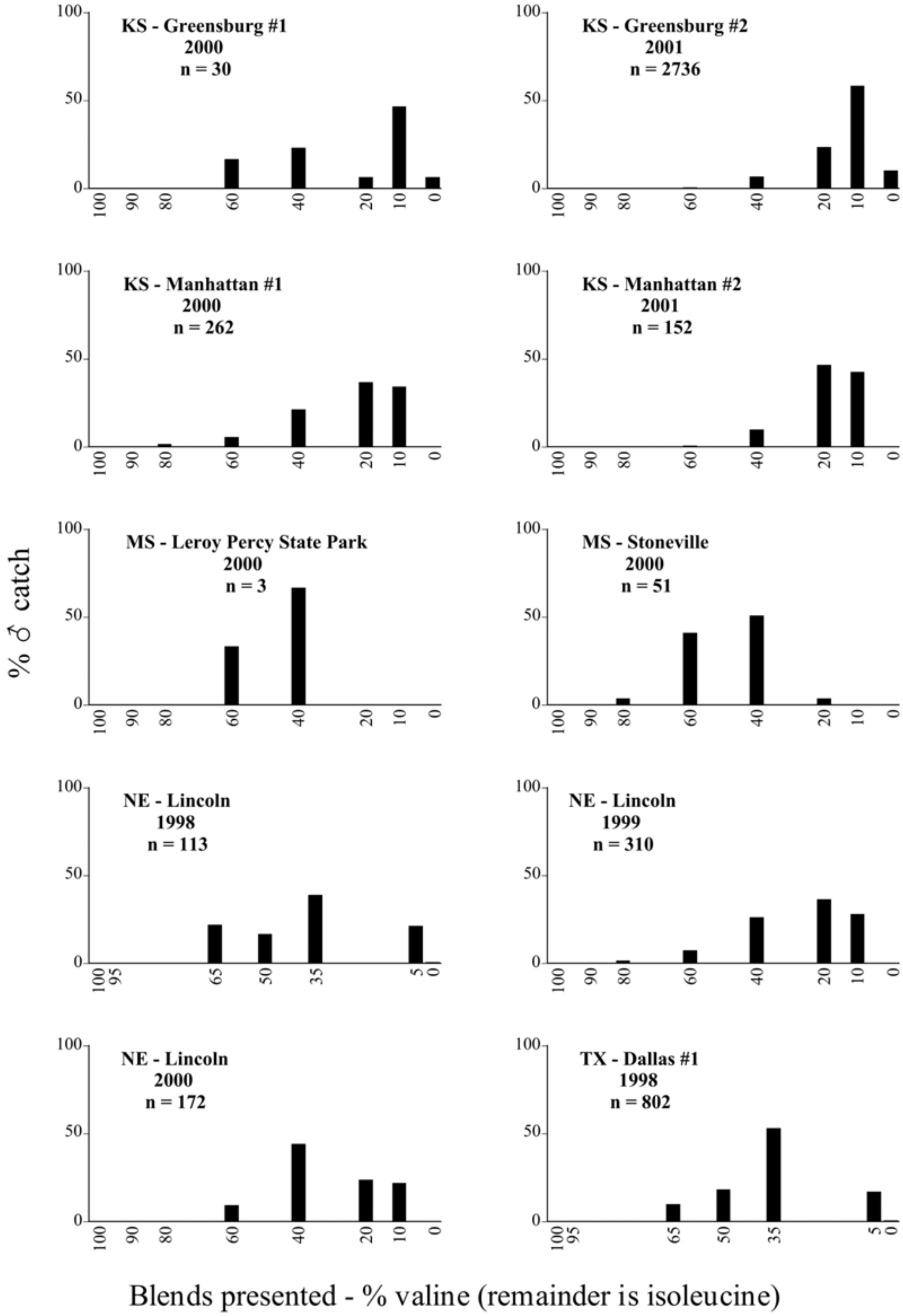


Figure 73a *P. crassissima* ♂ catches

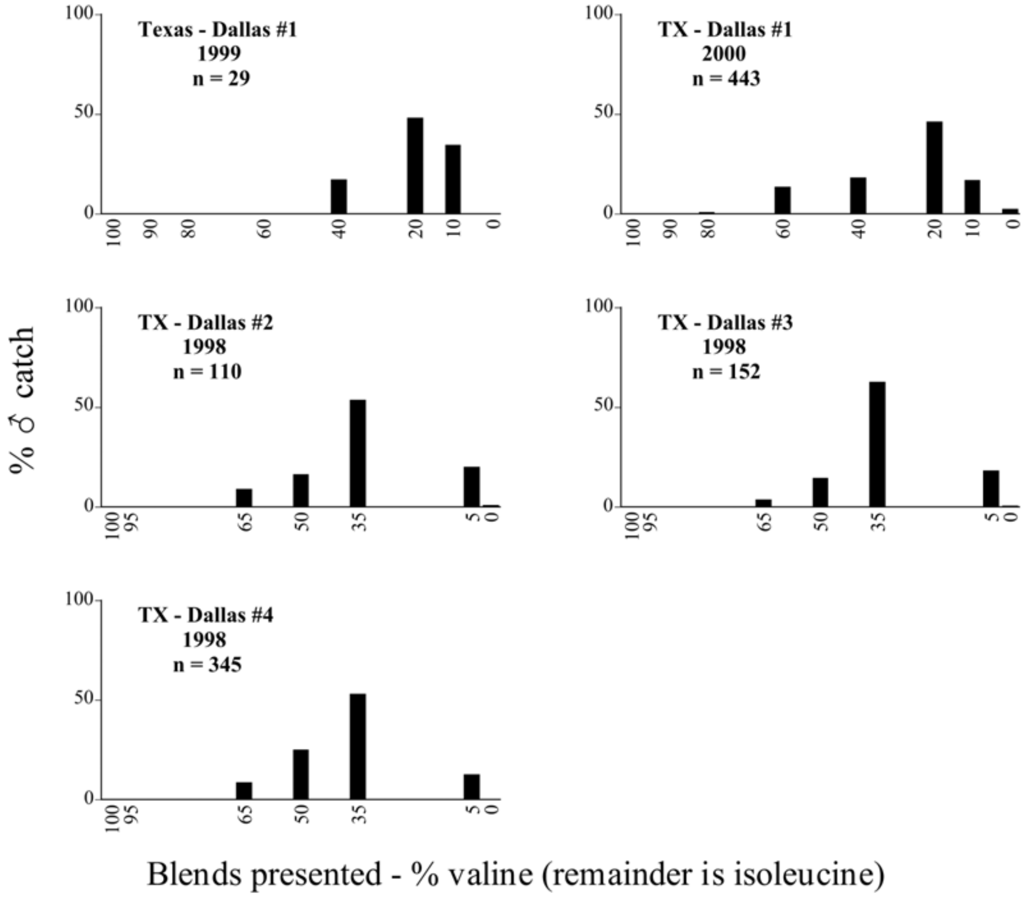


Figure 73b *P. crassissima* ♂ catches

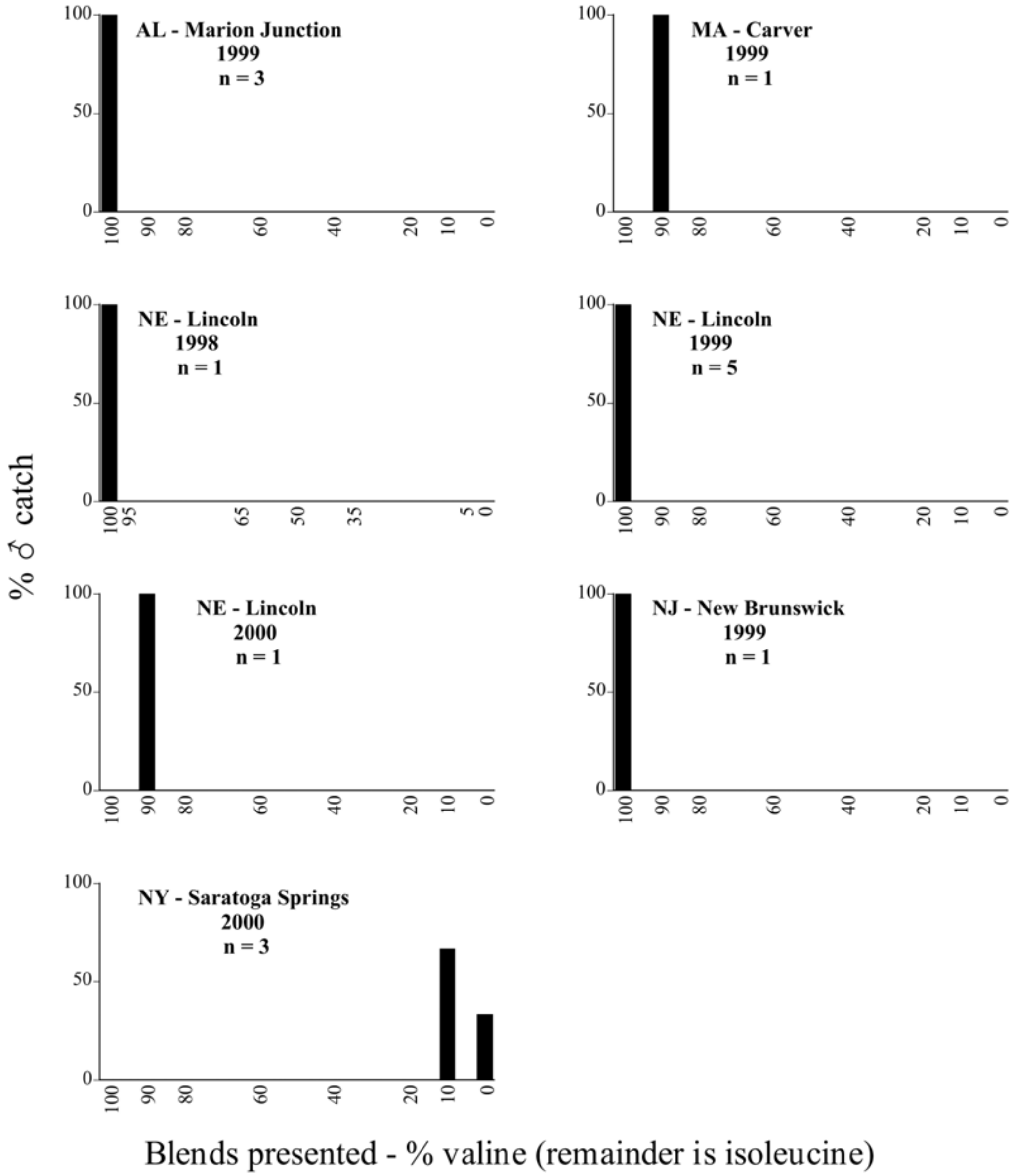


Figure 74 *P. crenulata* ♂ catches

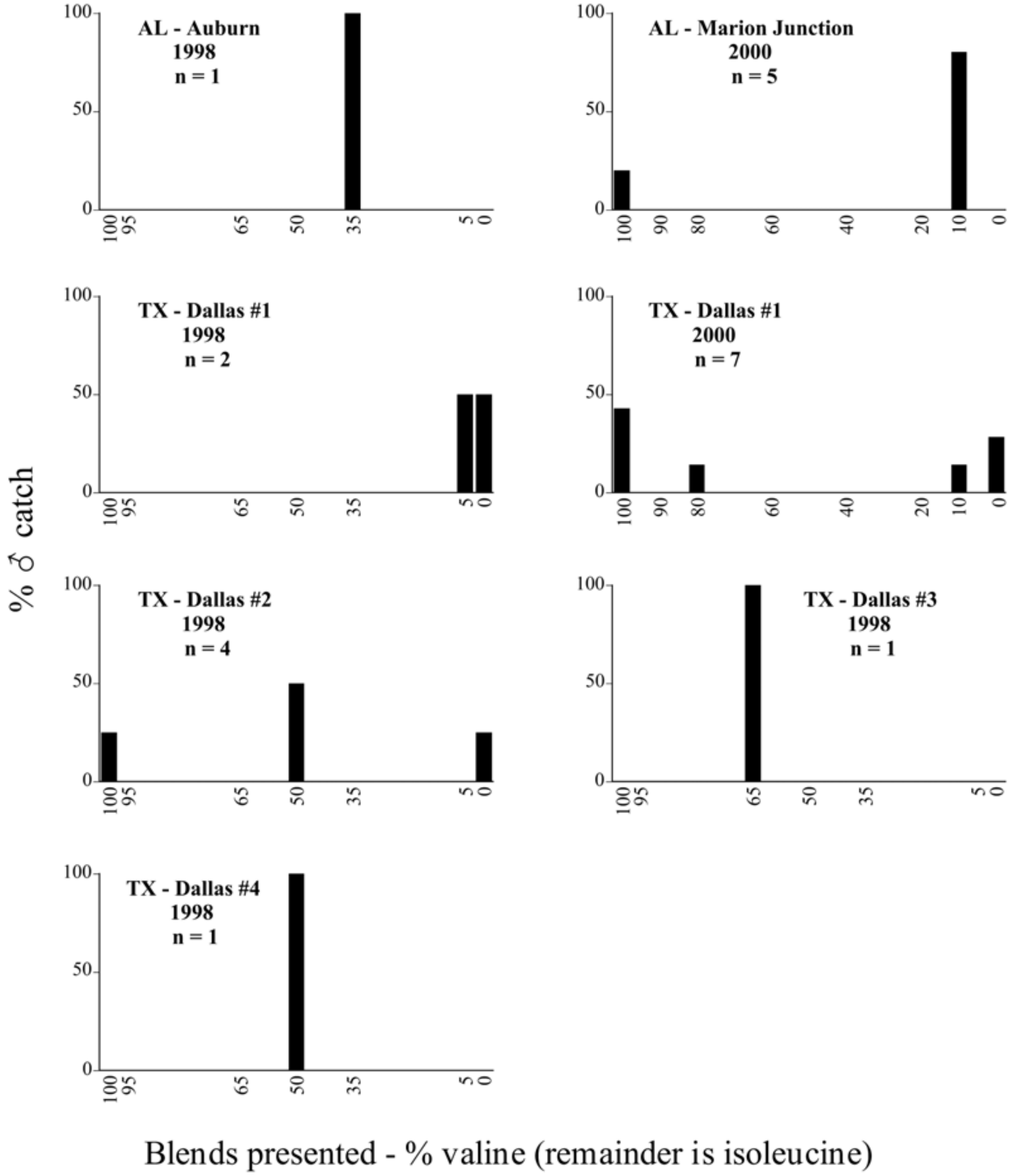


Figure 75 *P. crinita* ♂ catches

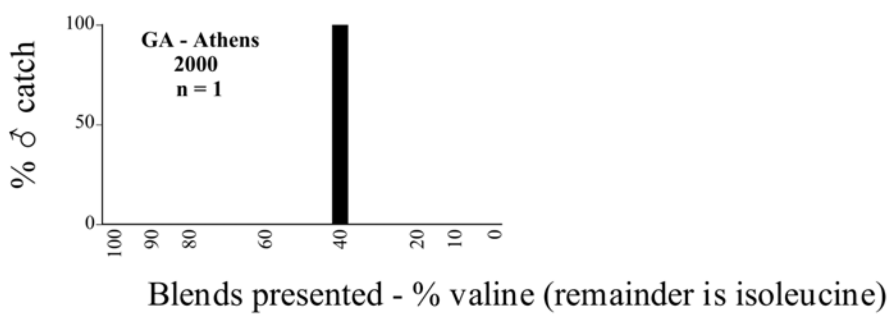


Figure 76 *P. curialis* ♂ catches

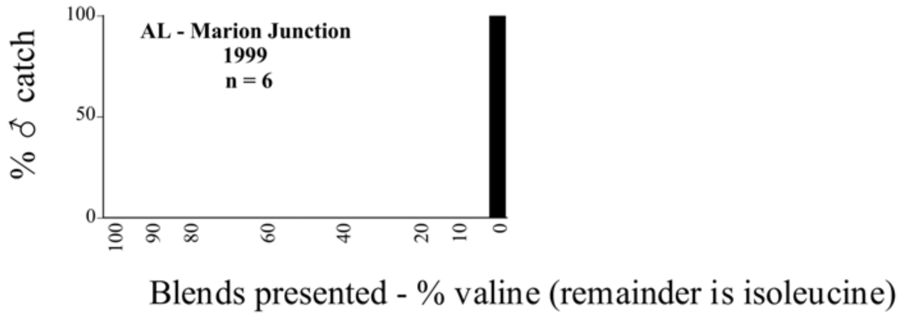


Figure 77 *P. davisi* ♂ catches

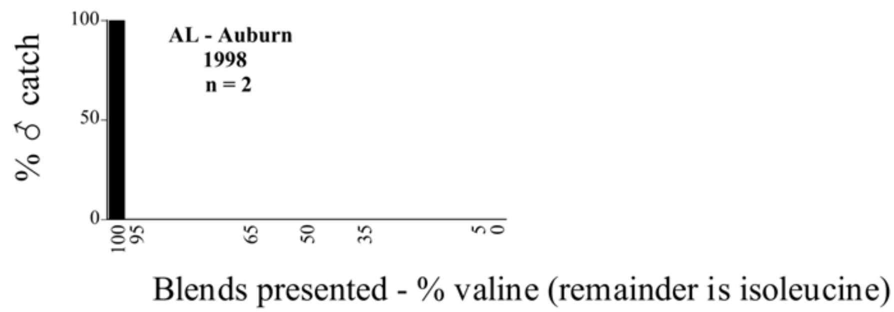


Figure 78 *P. diffinis* ♂ catches

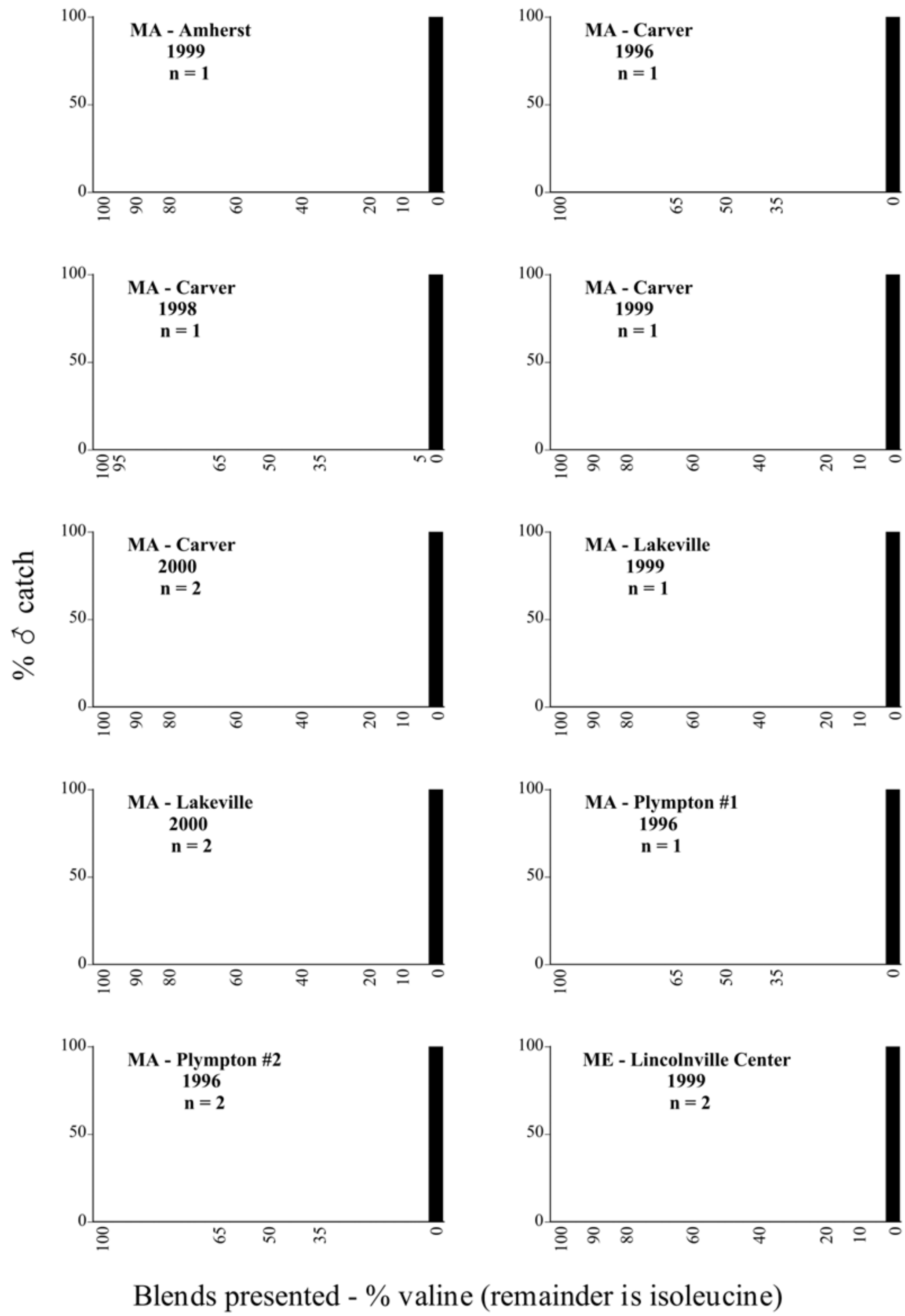


Figure 79a *P. drakei* ♂ catches

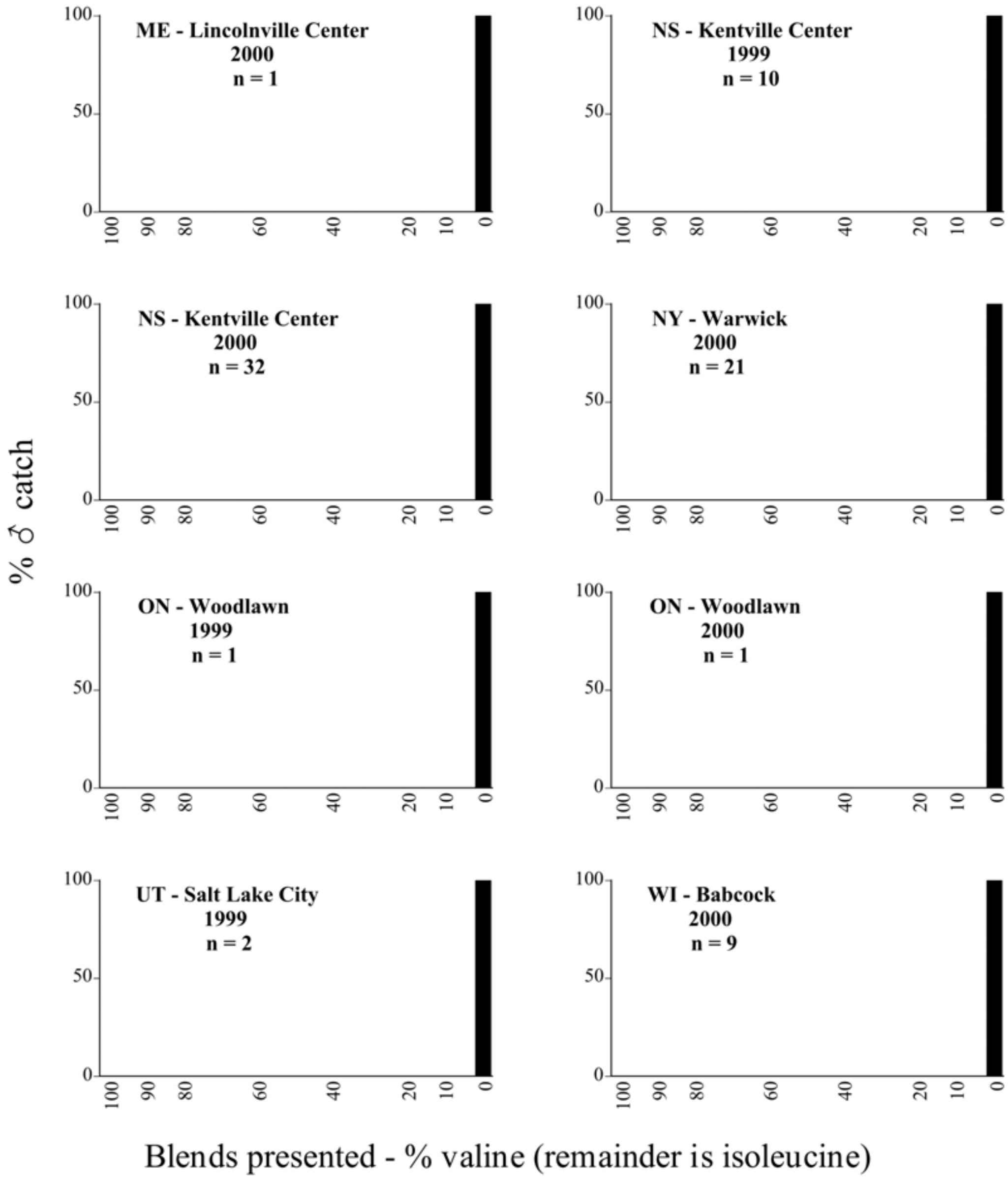


Figure 79b *P. drakei* ♂ catches

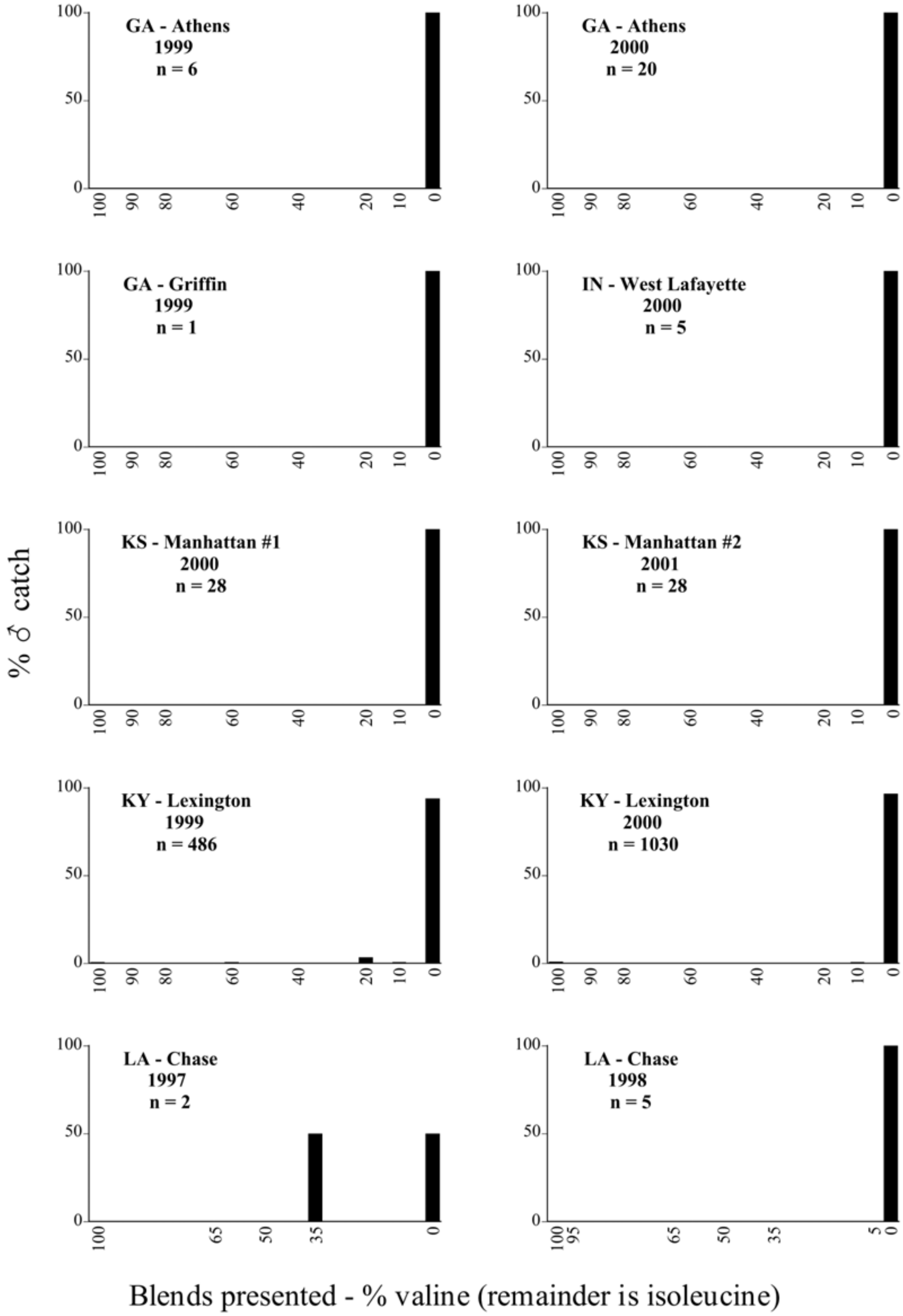


Figure 80a *P. ephilida* ♂ catches

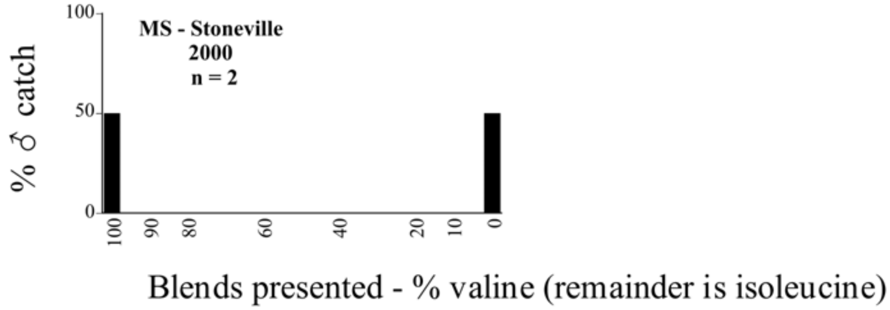


Figure 80b *P. ephilida* ♂ catches

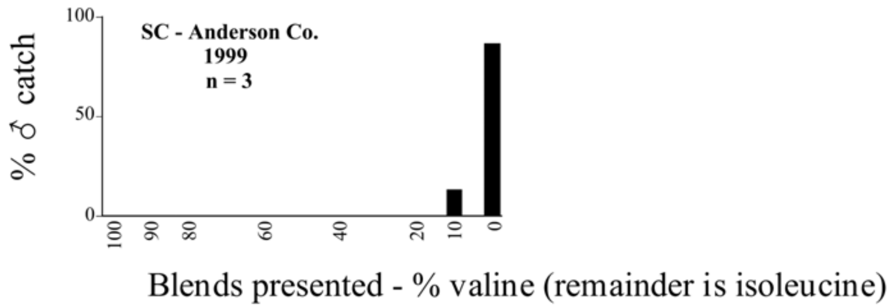


Figure 81 *P. fervida* ♂ catches

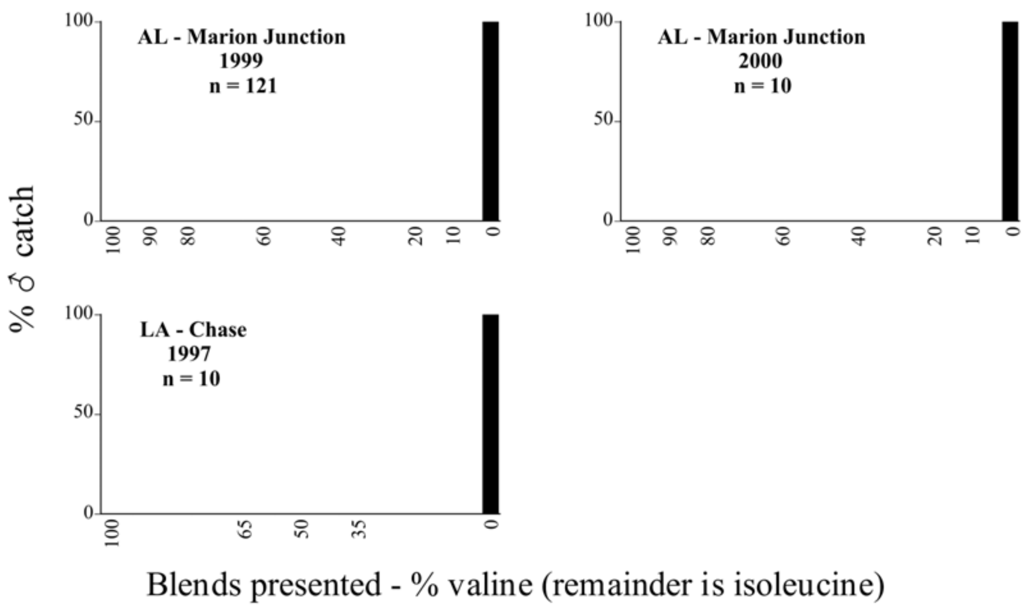


Figure 82 *P. forbesi* ♂ catches

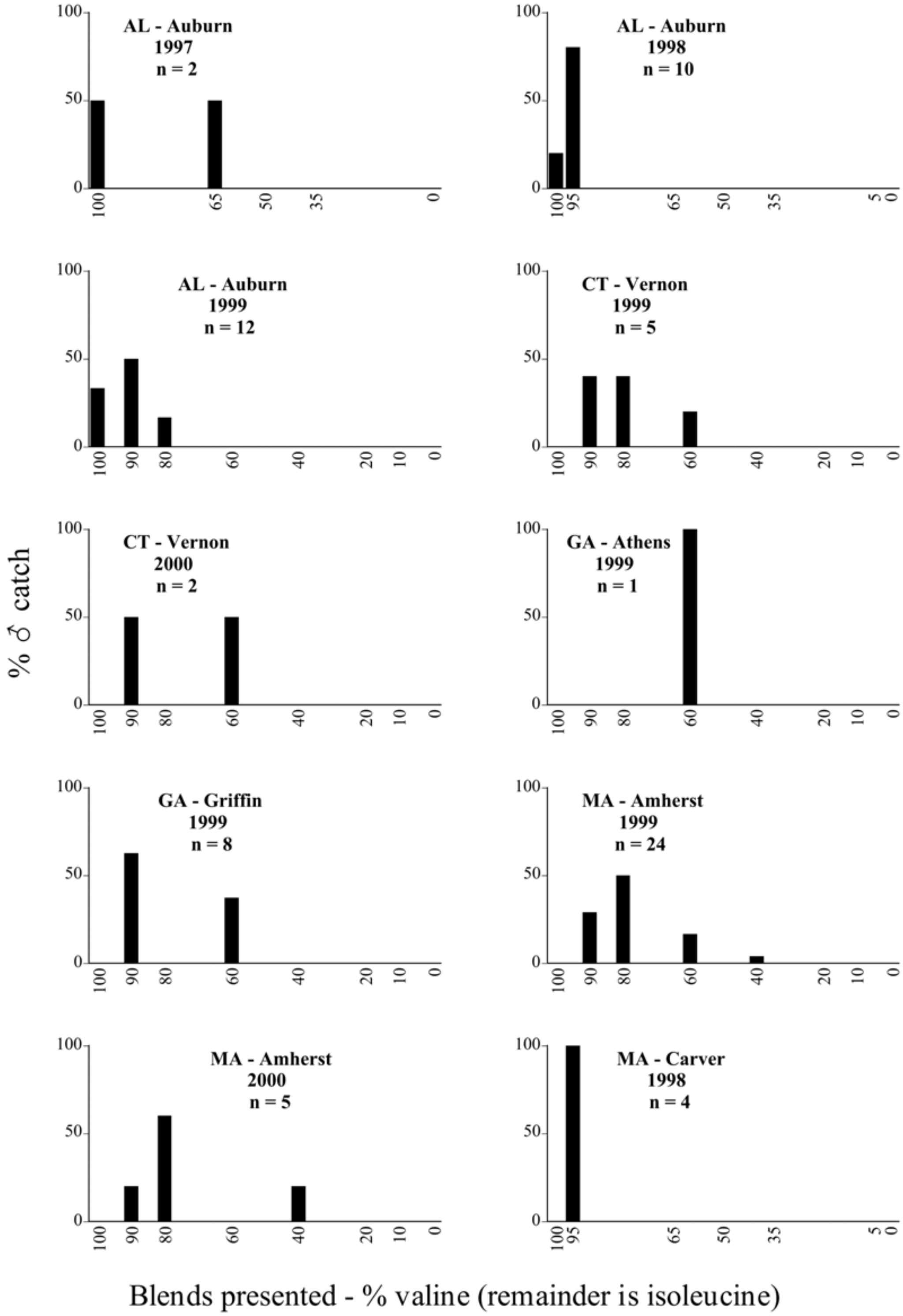


Figure 83a *P. forsteri* ♂ catches

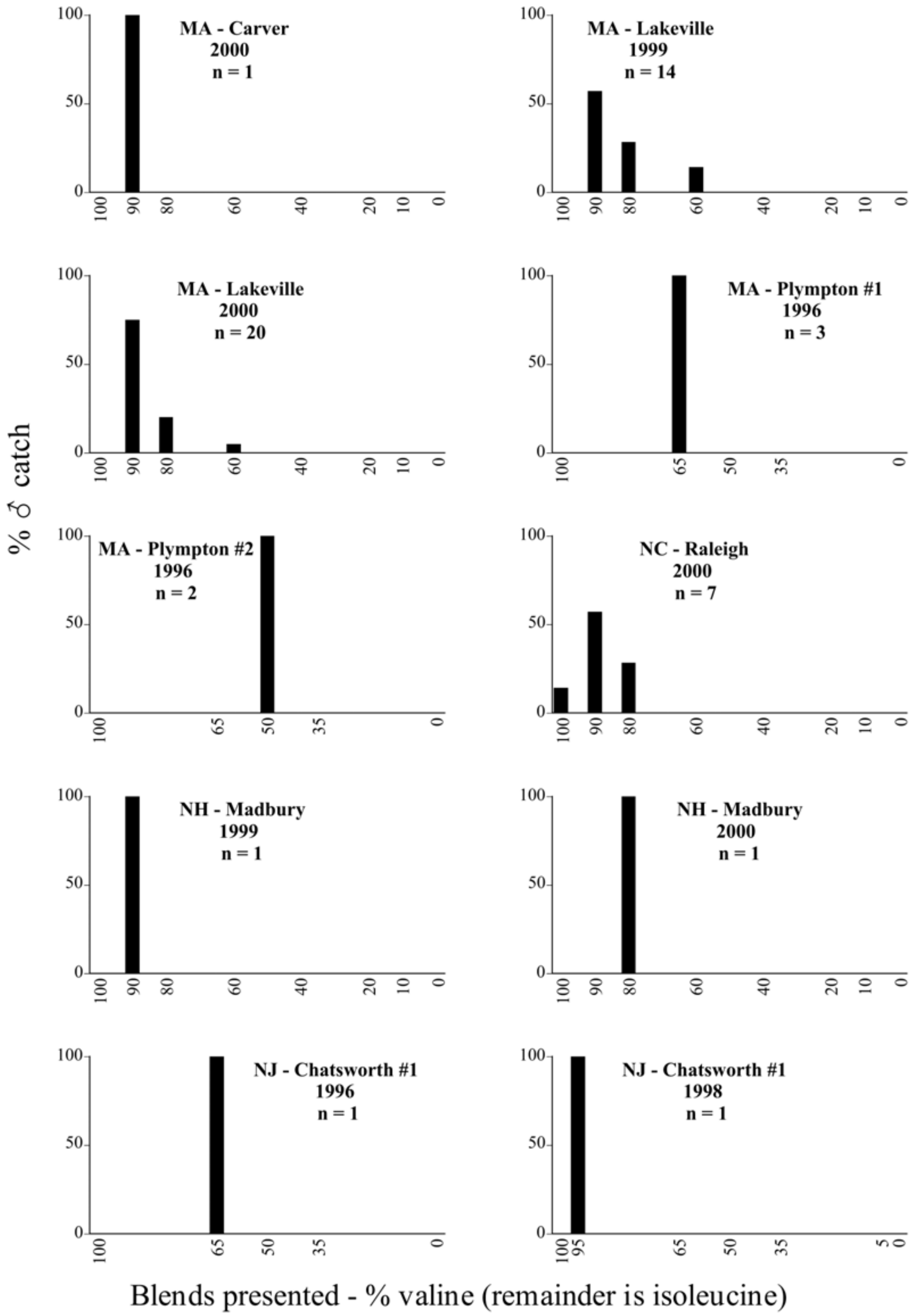


Figure 83b *P. forsteri* ♂ catches

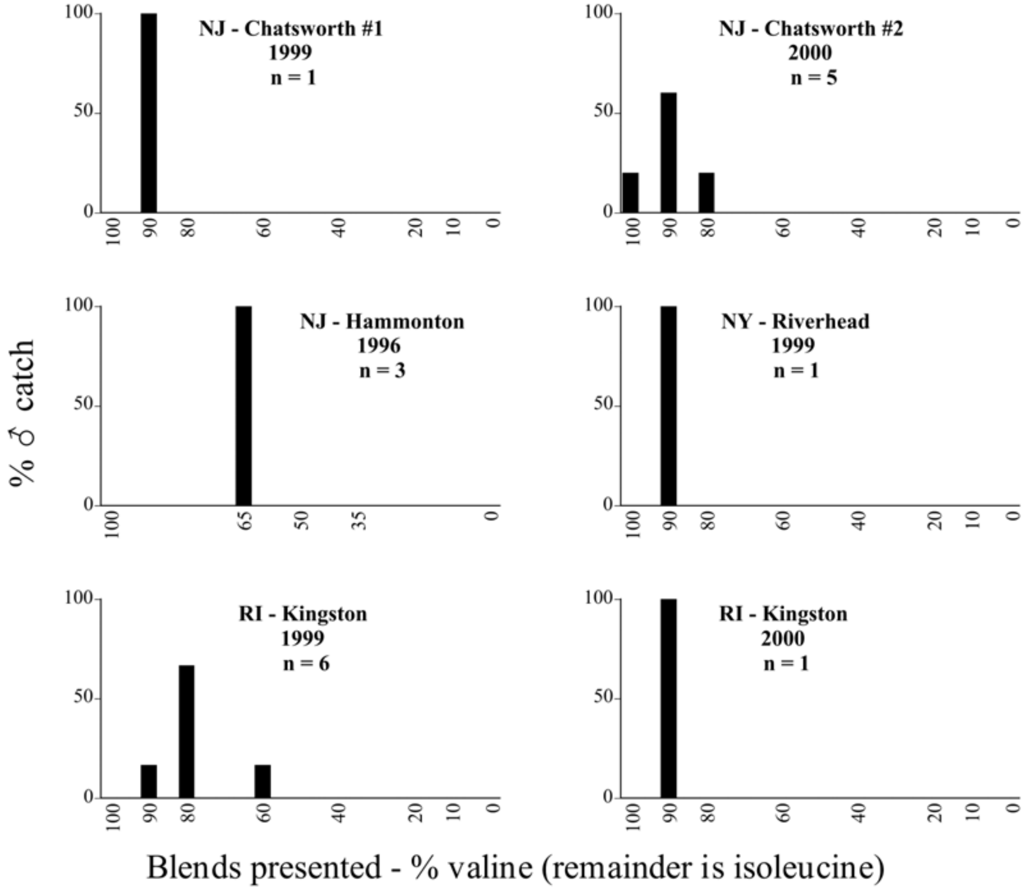


Figure 83c *P. forsteri* ♂ catches

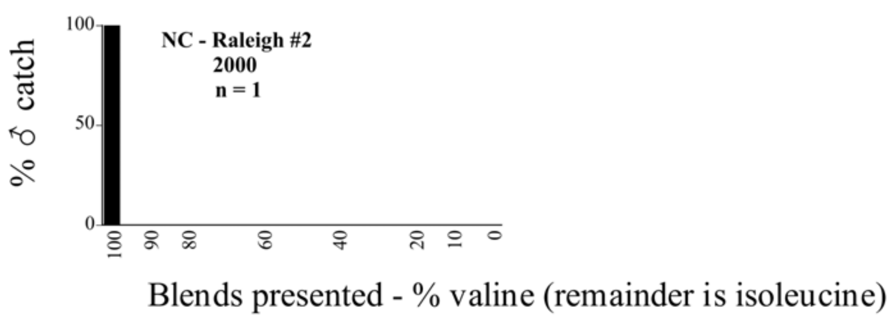


Figure 84 *P. foxii* ♂ catches

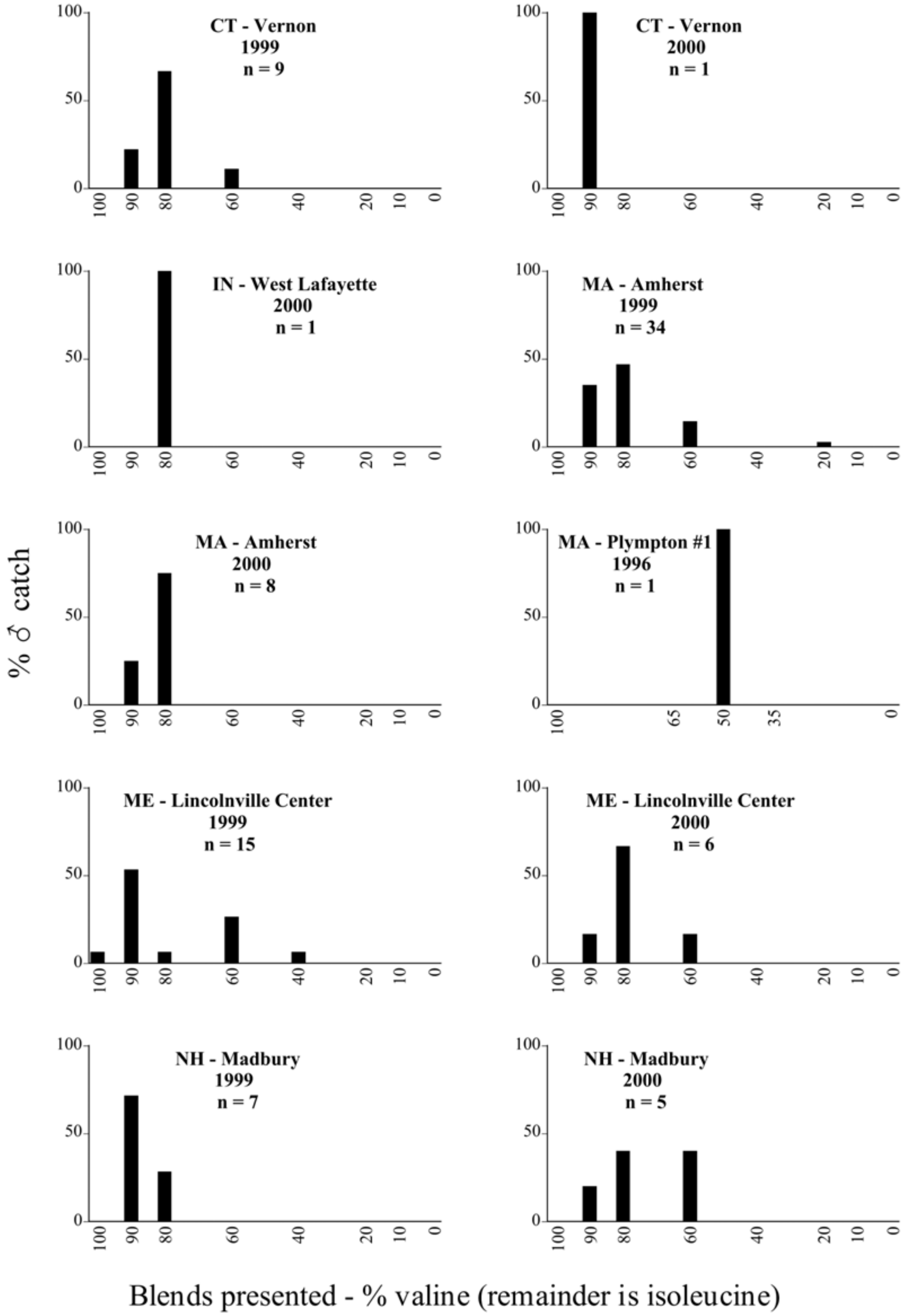


Figure 85a *P. fraterna* ♂ catches

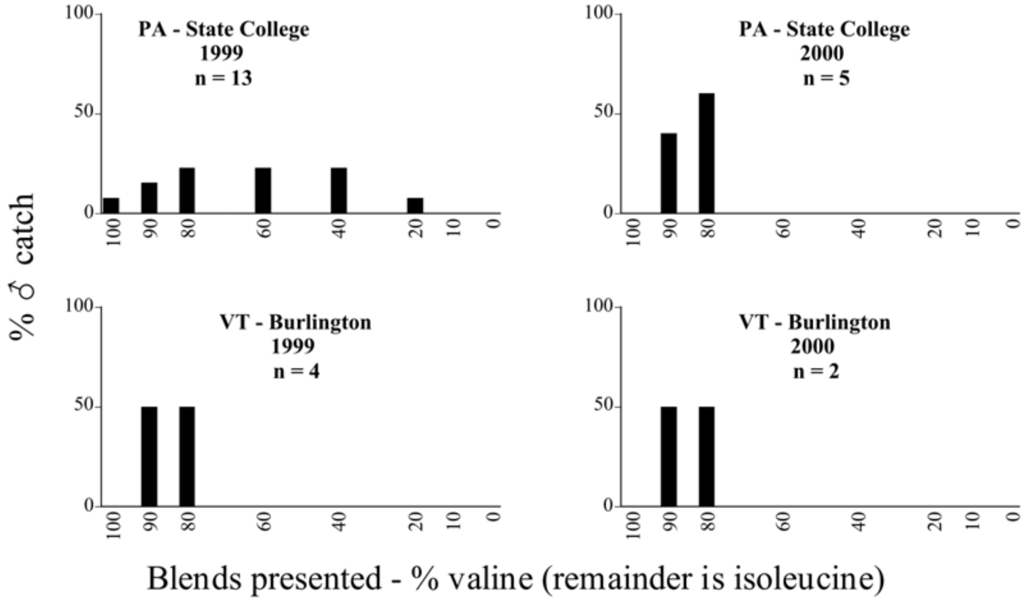


Figure 85b *P. fraterna* ♂ catches

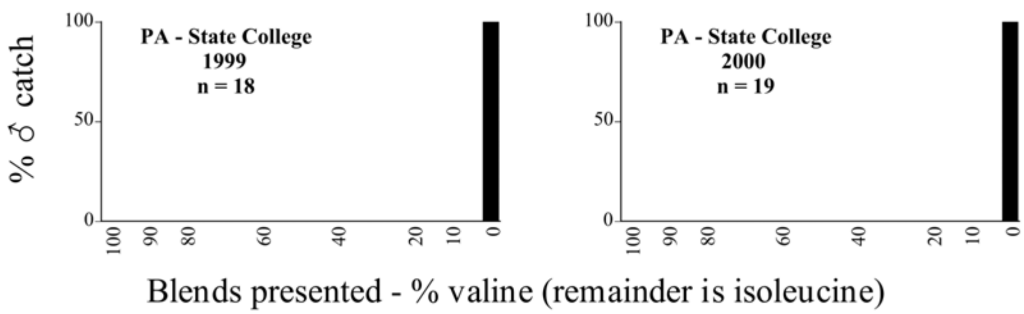


Figure 86 *P. fraterna*-like ♂ catches

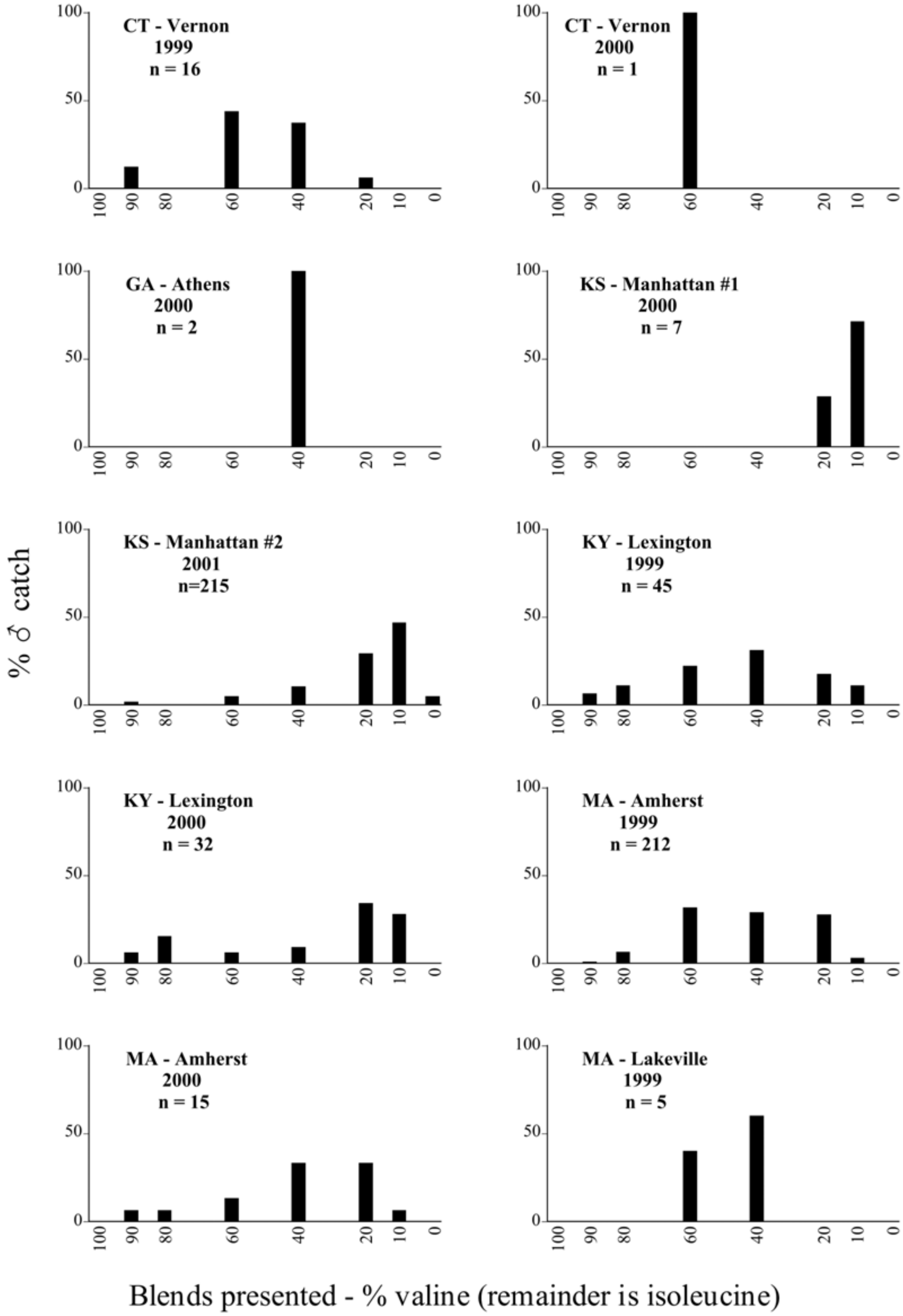


Figure 87a *P. fusca* ♂ catches

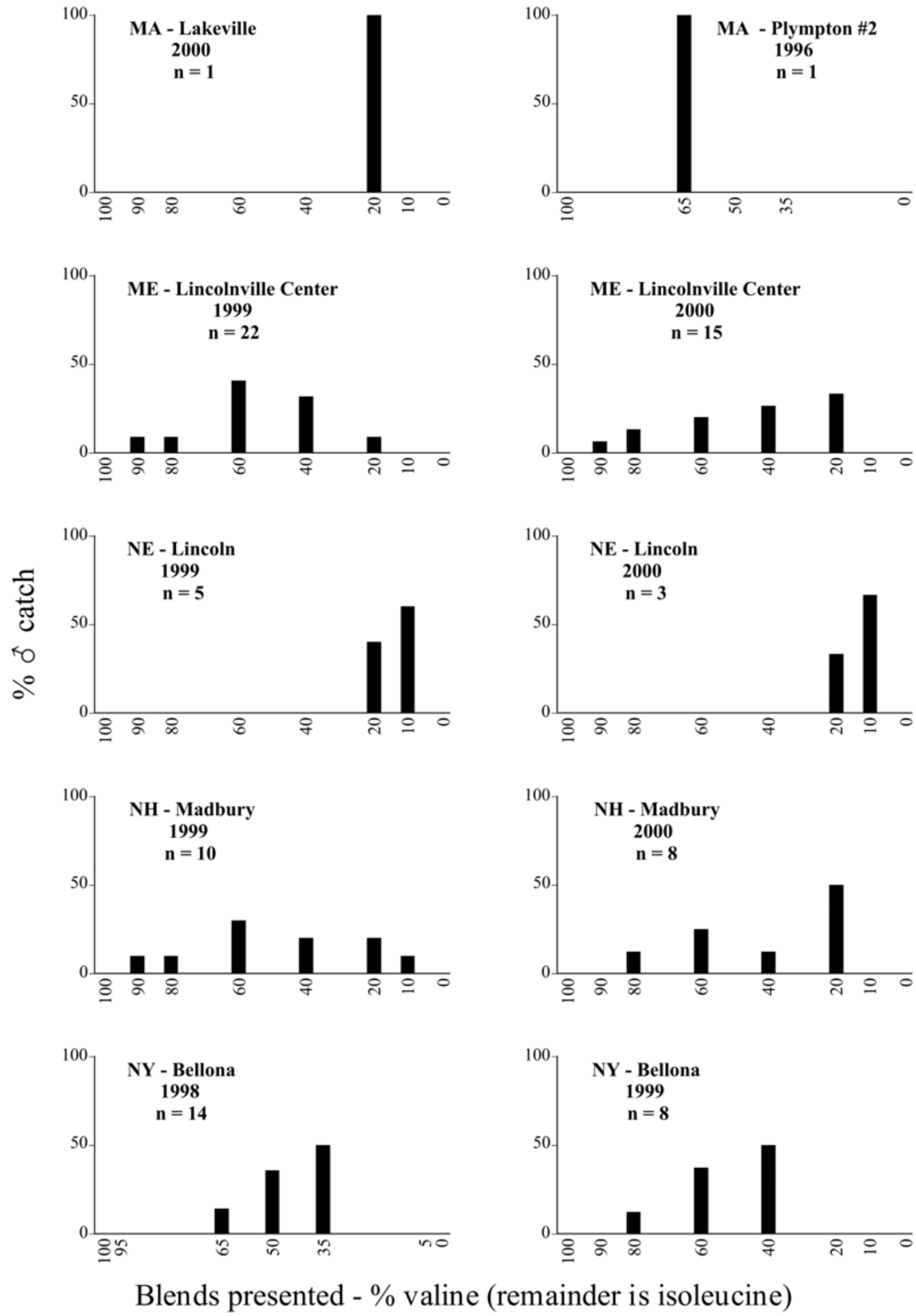


Figure 87b *P. fusca* ♂ catches

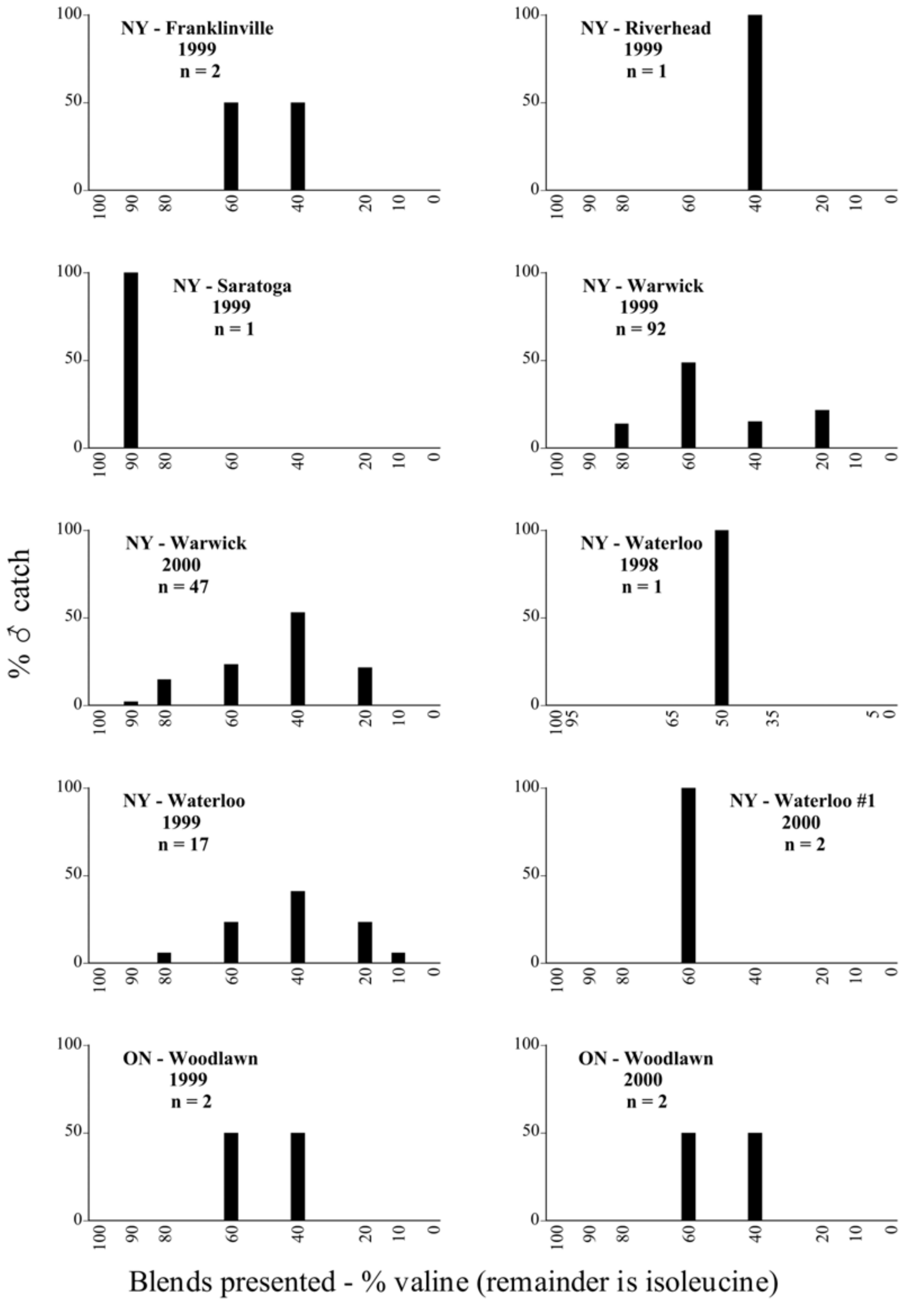


Figure 87c *P. fusca* ♂ catches

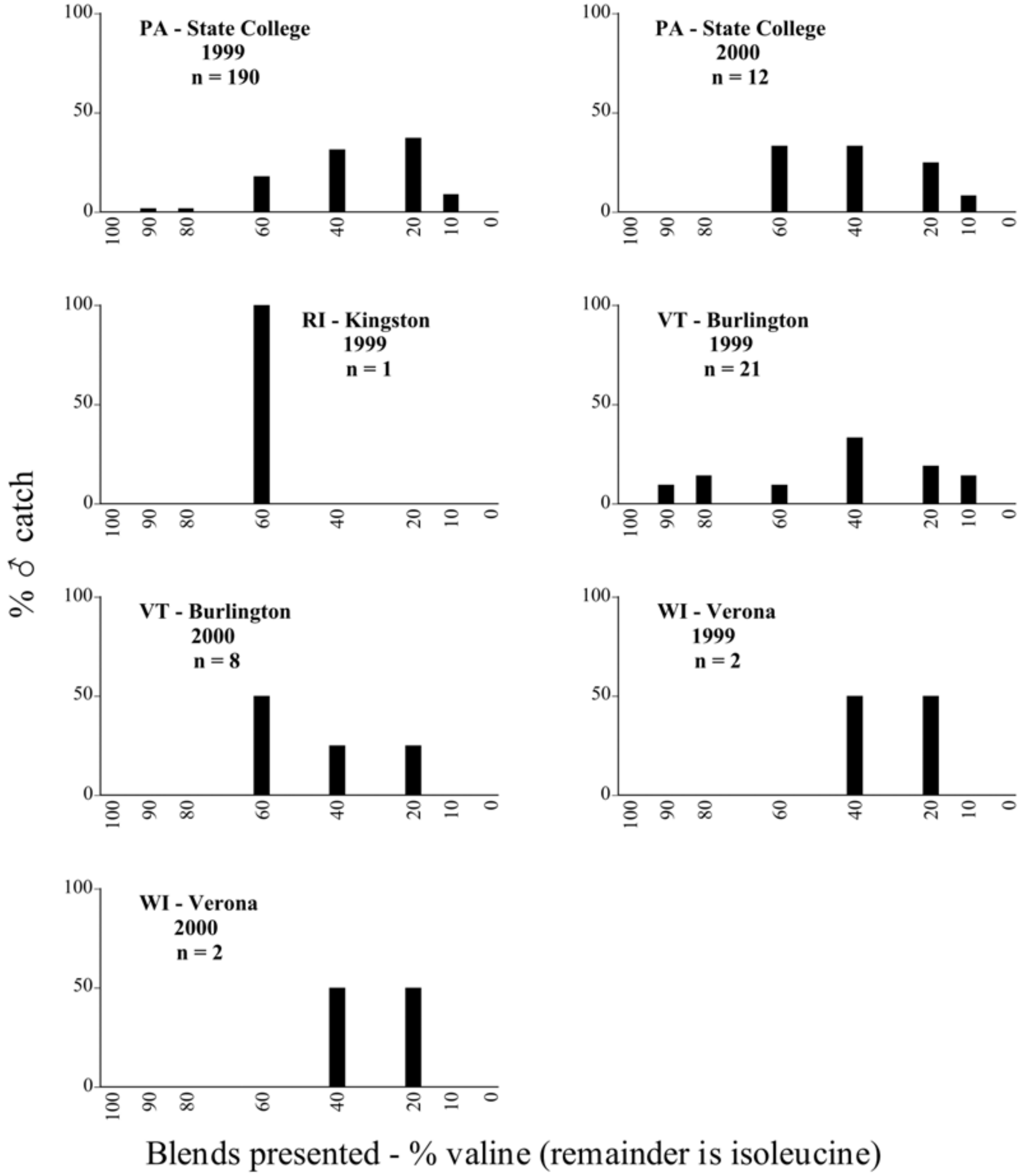


Figure 87d *P. fusca* ♂ catches

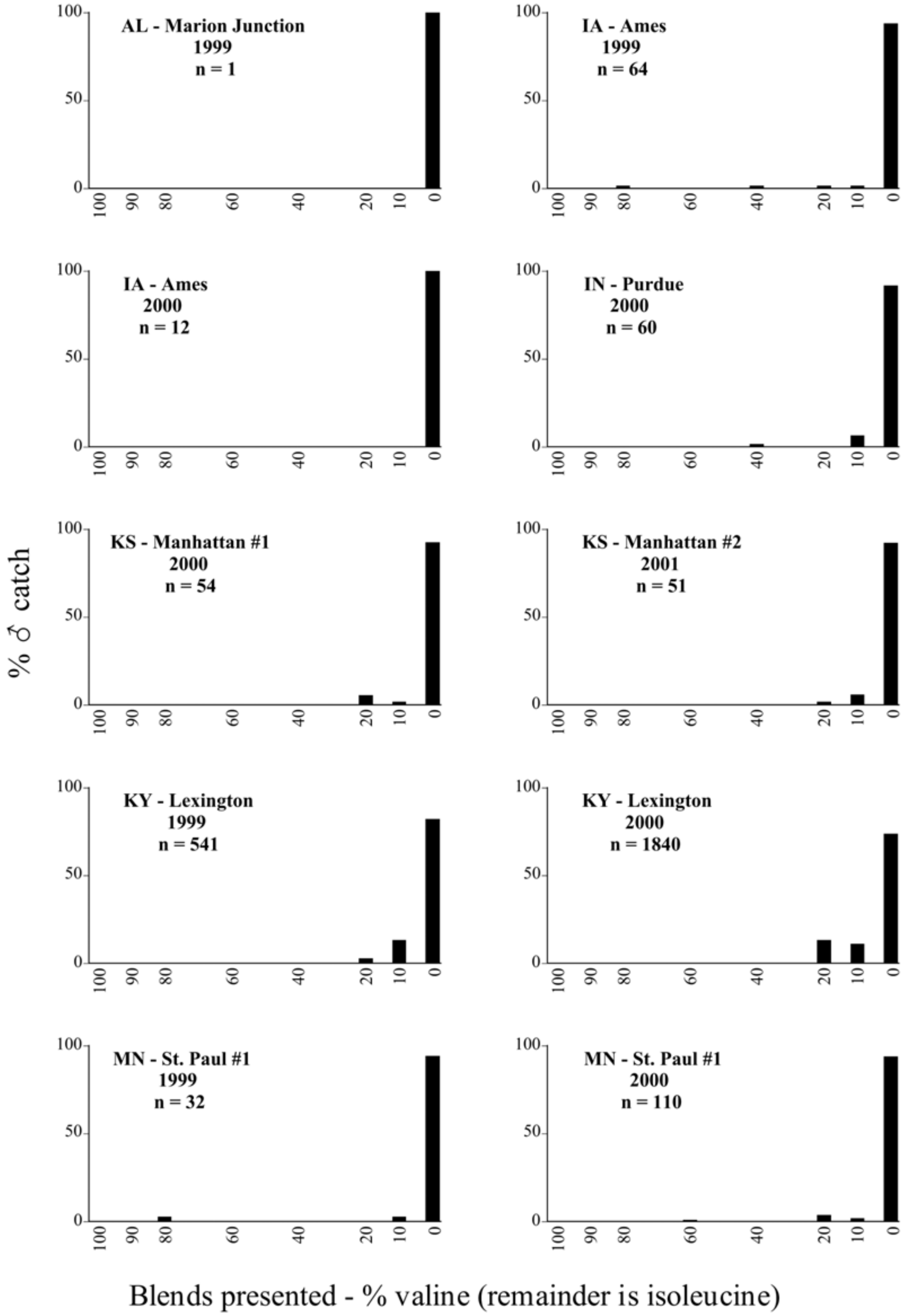


Figure 88a *P. futilis* ♂ catches

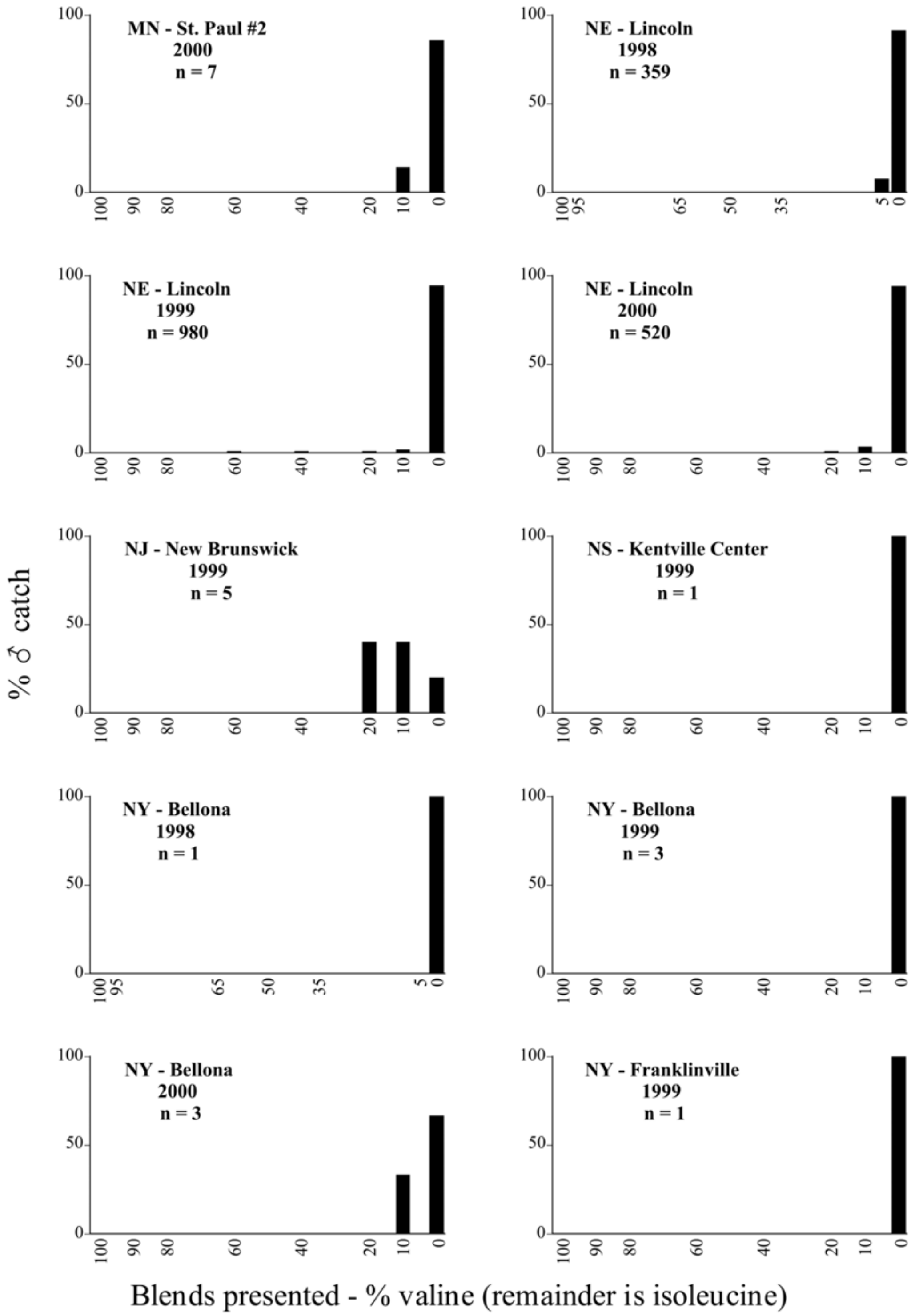


Figure 88b *P. futilis* ♂ catches

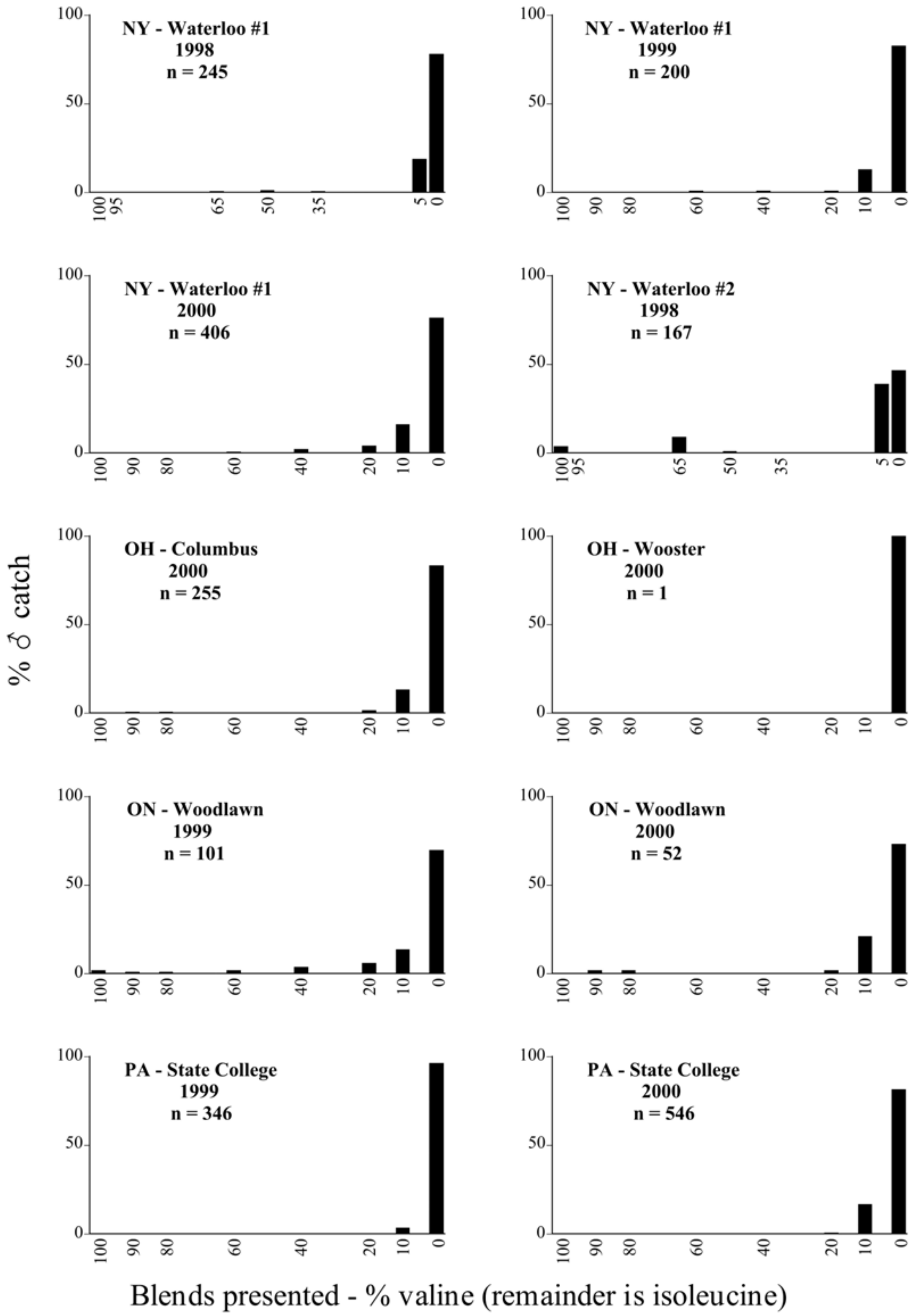


Figure 88c *P. futilis* ♂ catches

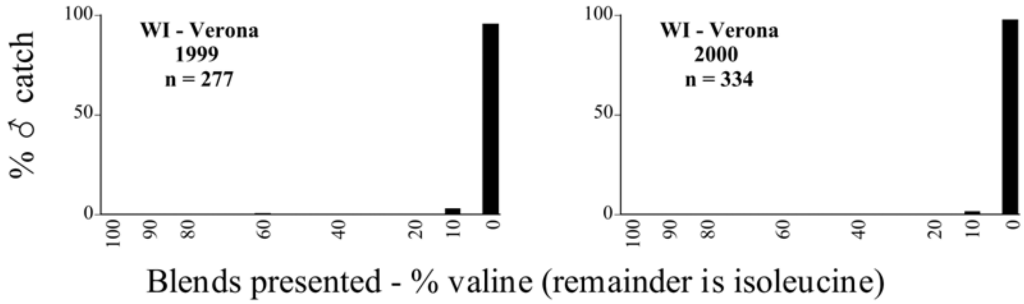


Figure 88d *P. futilis* ♂ catches

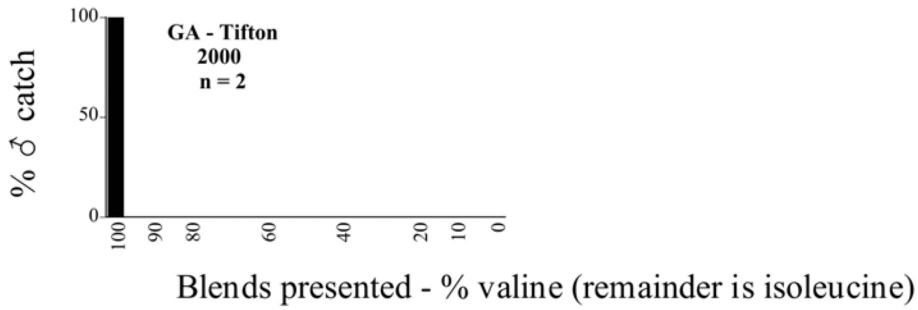


Figure 89 *P. (Phytalus) georgiana* ♂ catches

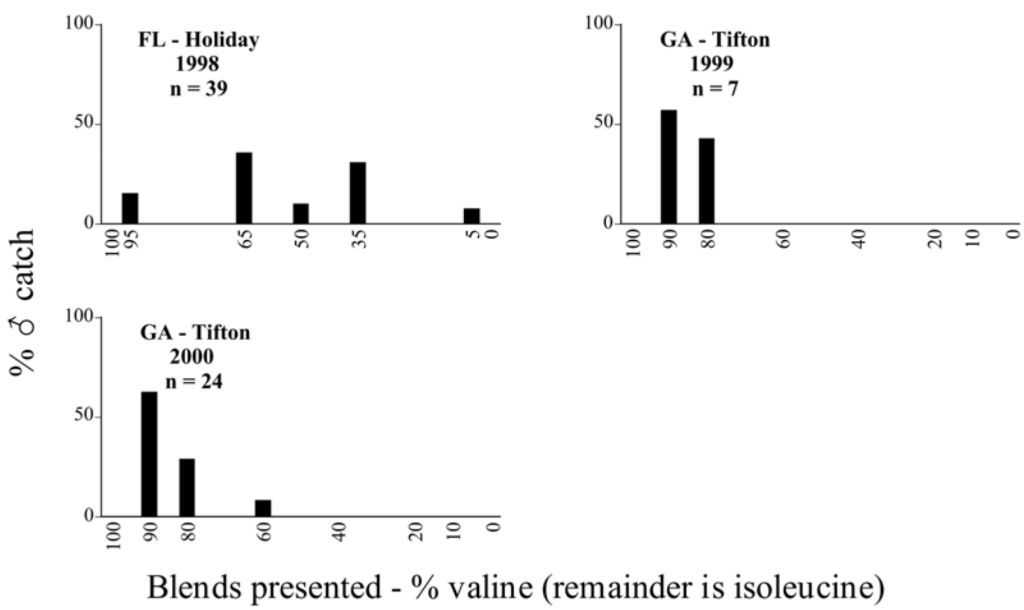


Figure 90 *P. glaberrima* ♂ catches

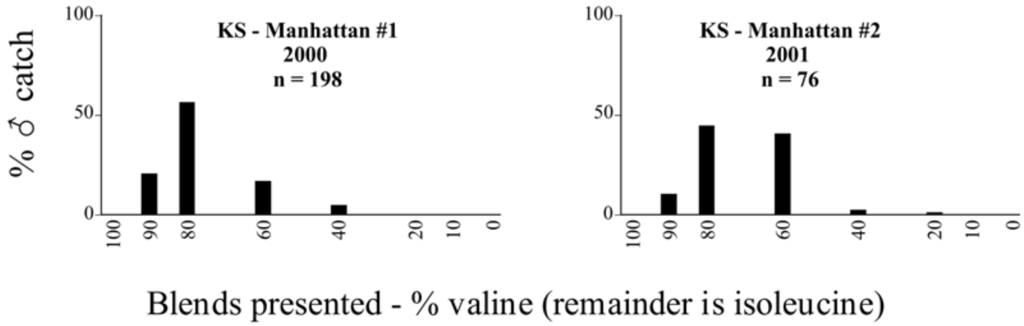


Figure 91 *P. glabricula* ♂ catches

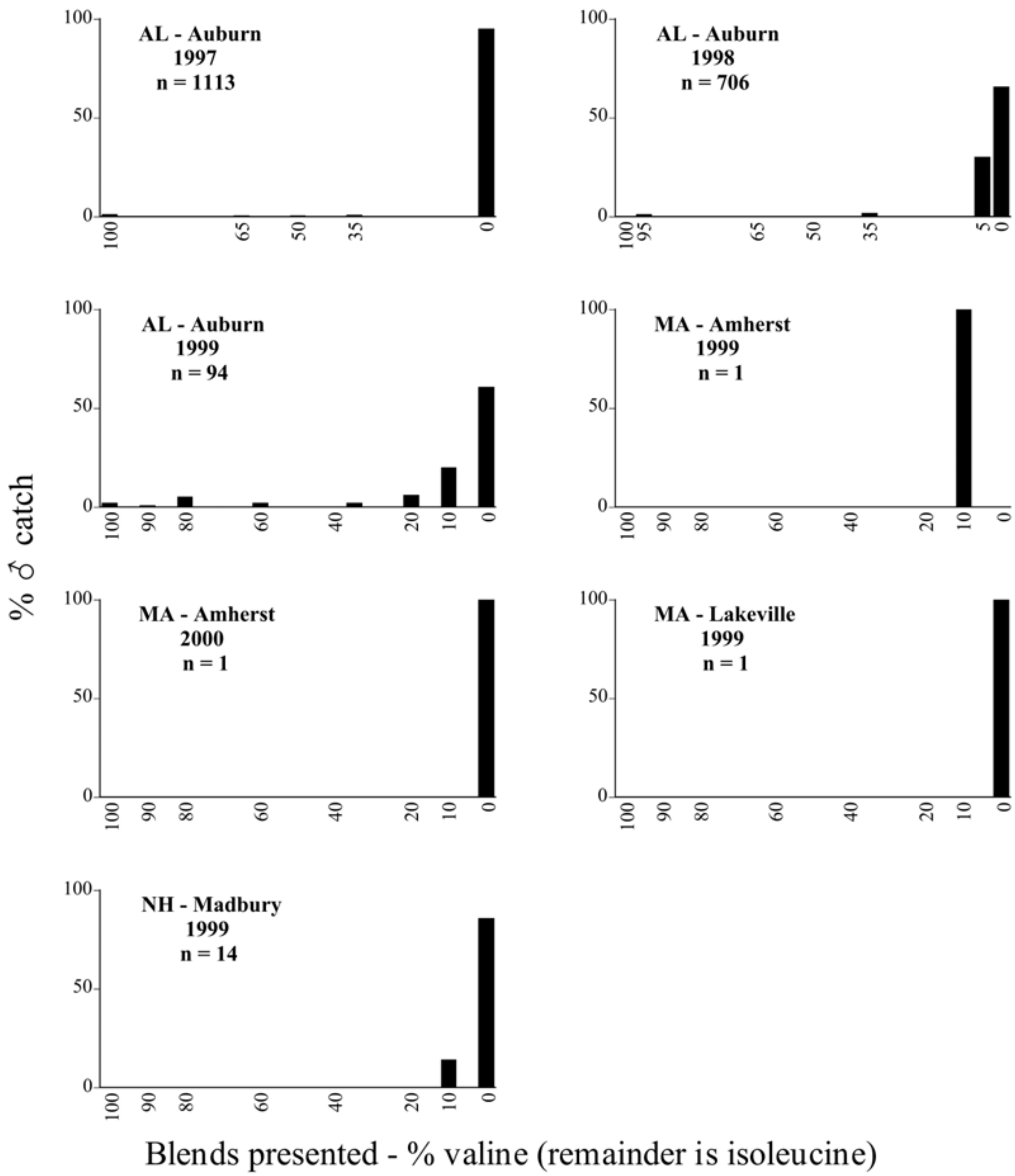


Figure 92 *P. gracilis* ♂ catches

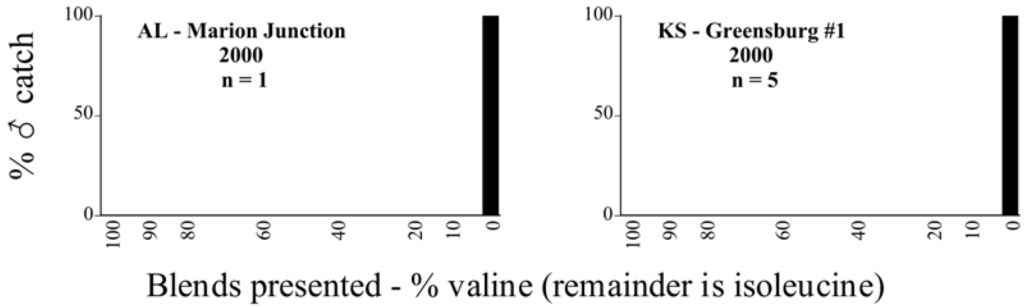


Figure 93 *P. gracilis* var. *angulata* ♂ catches

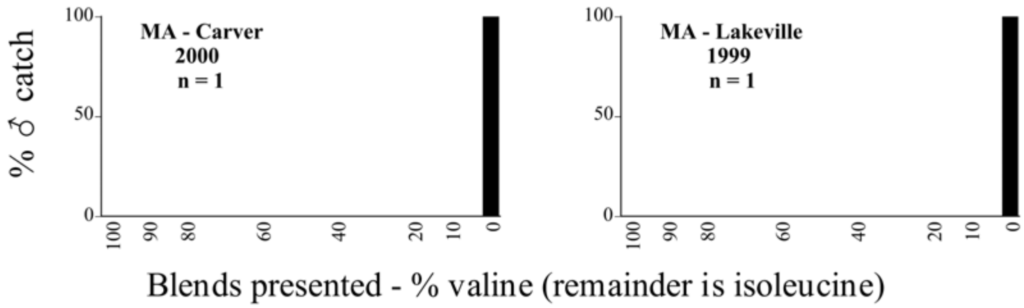


Figure 94 *P. hirsuta* ♂ catches

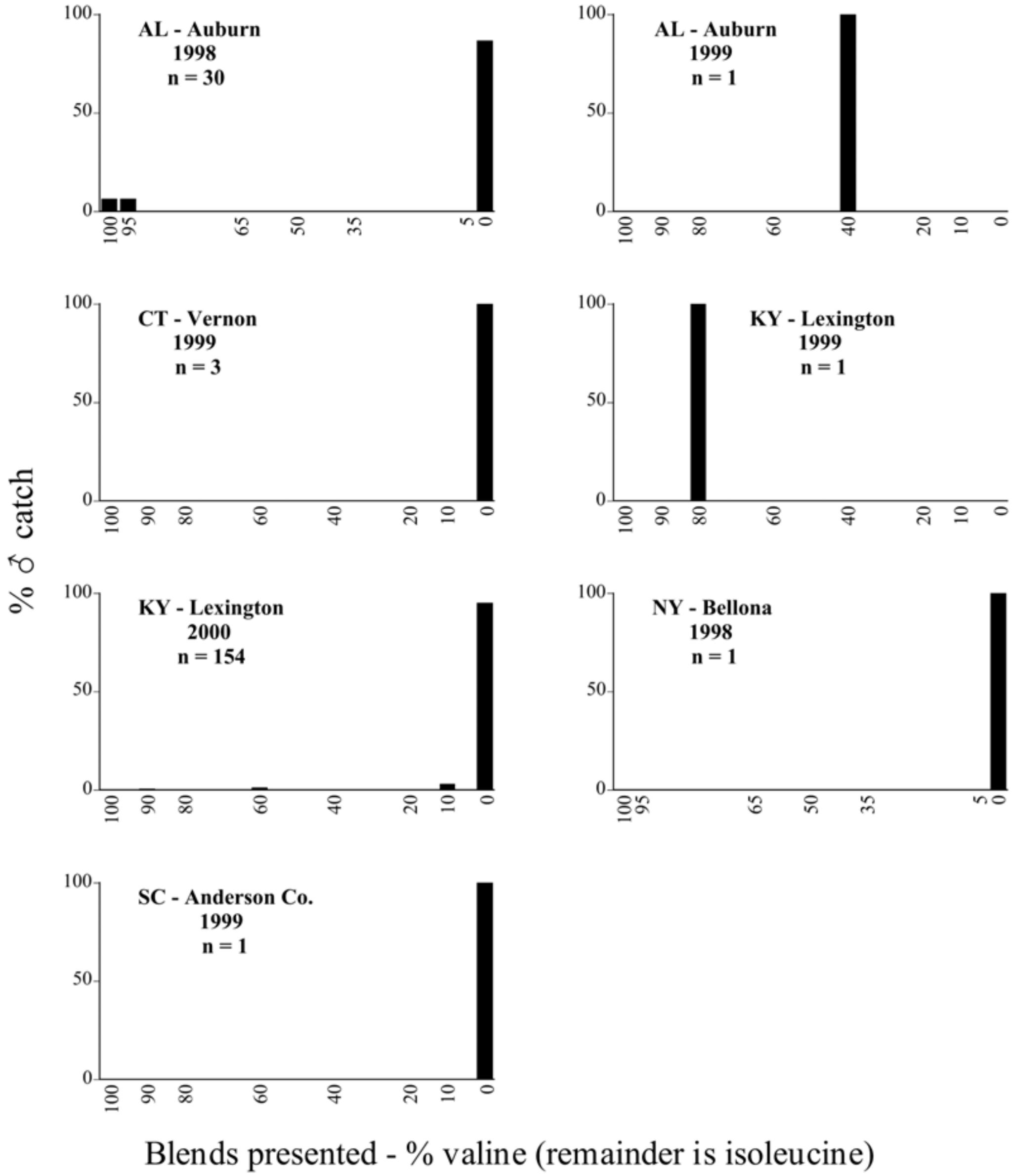


Figure 95 *P. hirticula* ♂ catches

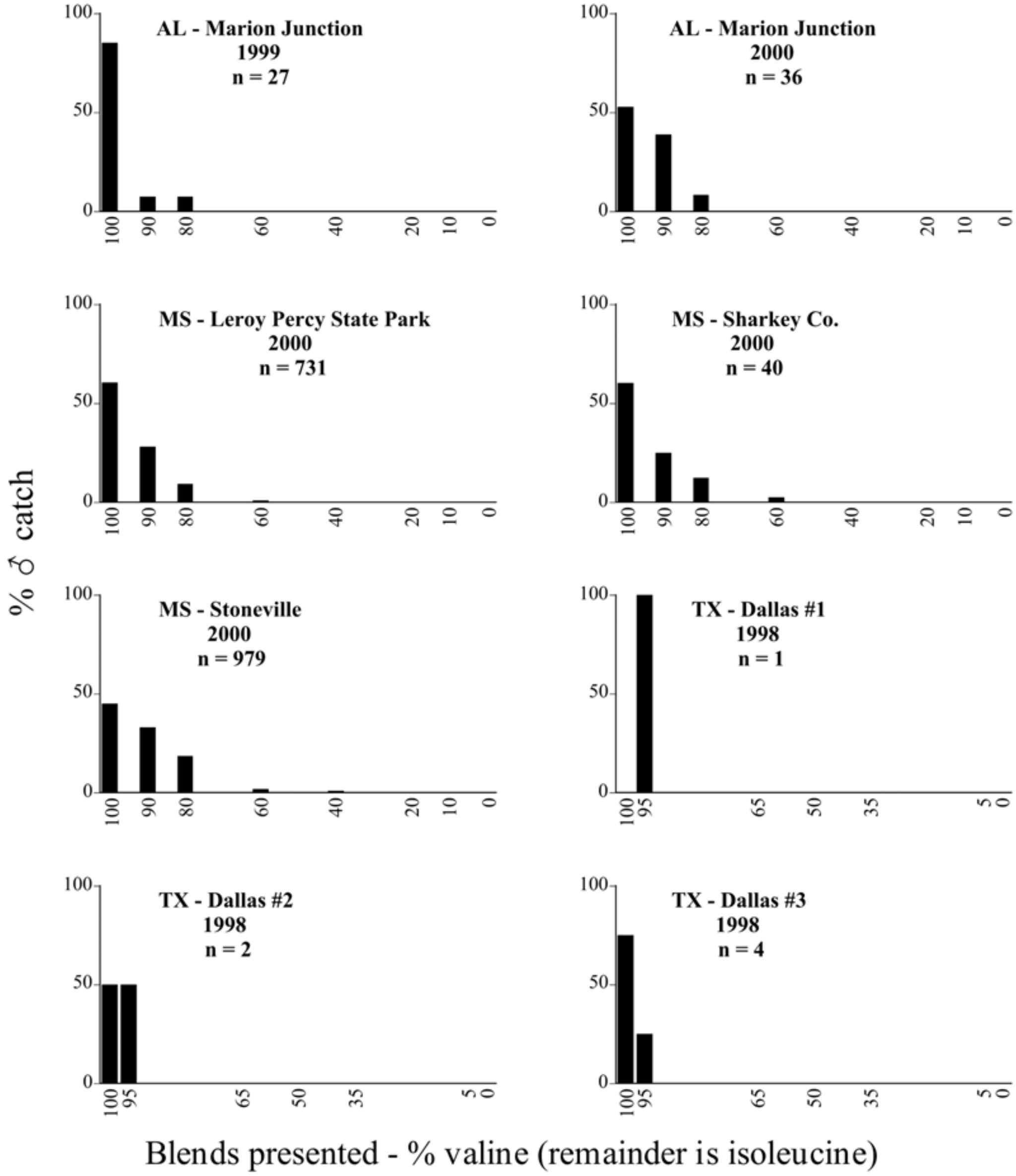


Figure 96 *P. hirtiventris* ♂ catches

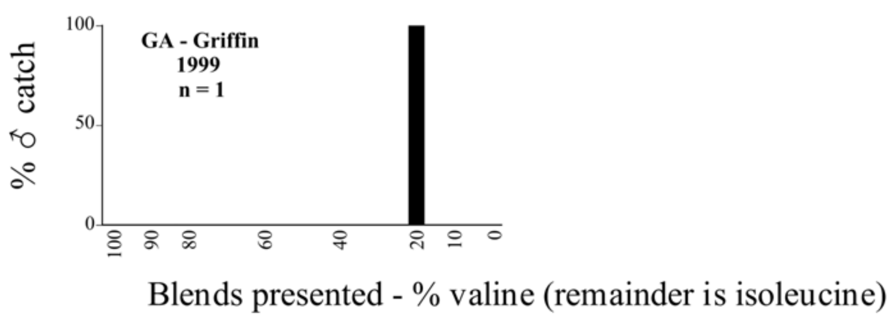


Figure 97 *P. ilicis* ♂ catches

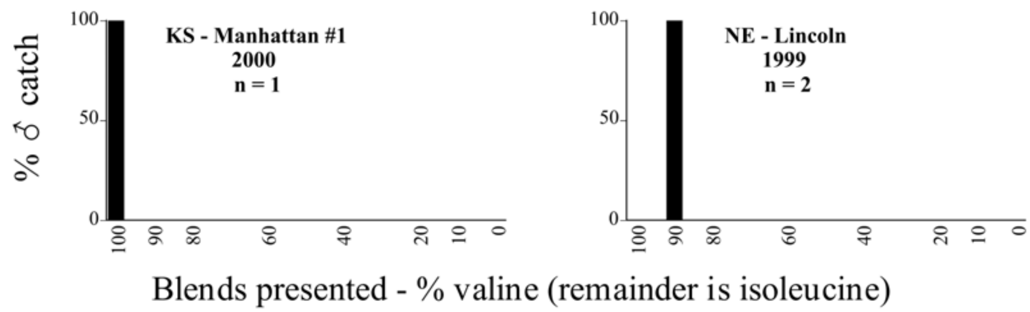


Figure 98 *P. implicita* ♂ catches

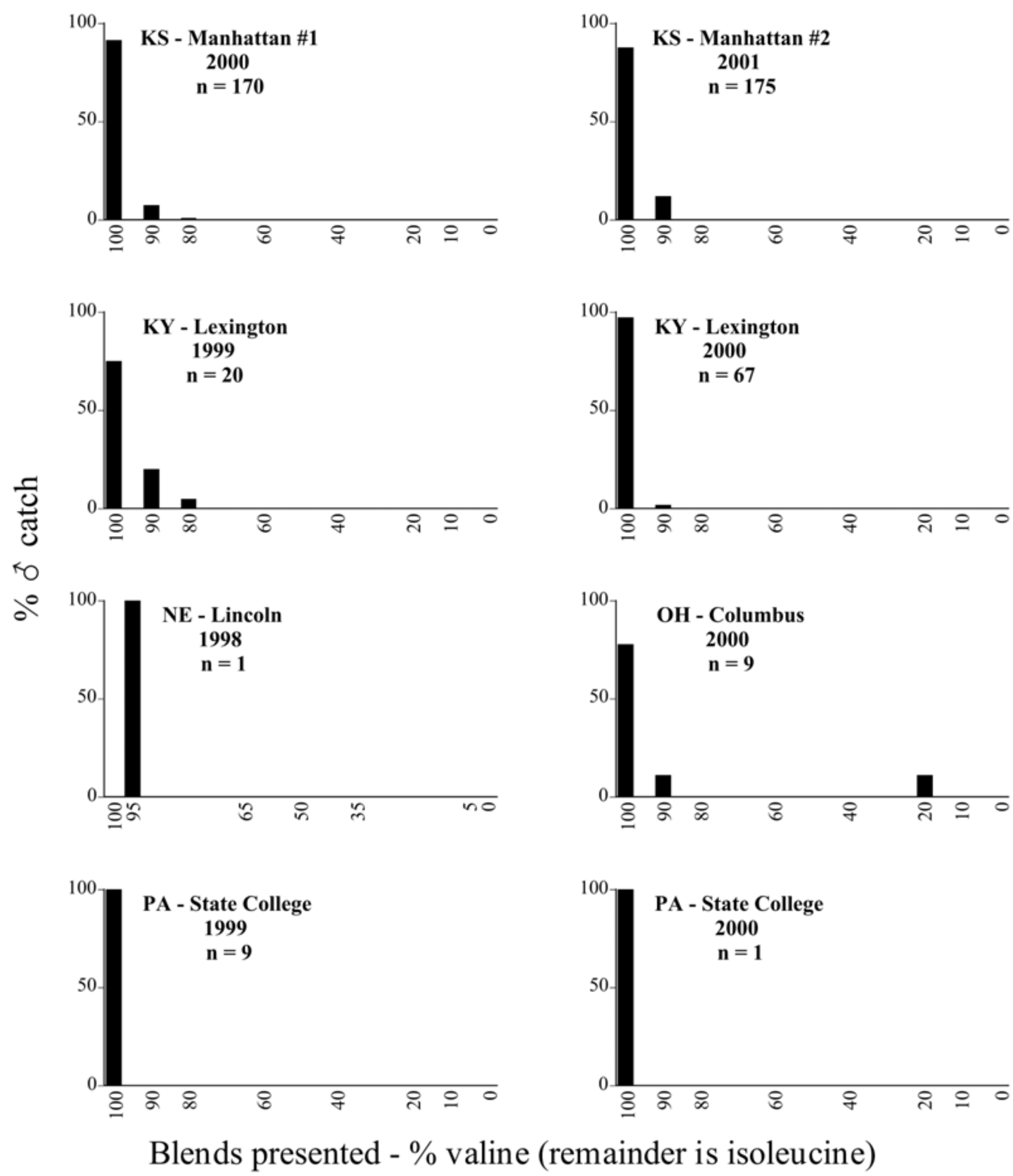


Figure 99 *P. inversa* ♂ catches

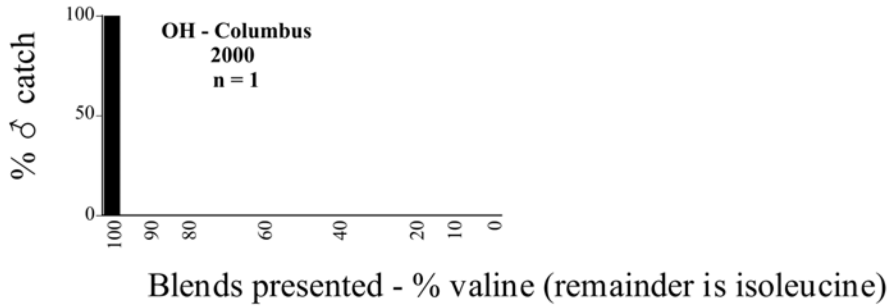


Figure 100 *P. kentuckiana* ♂ catches

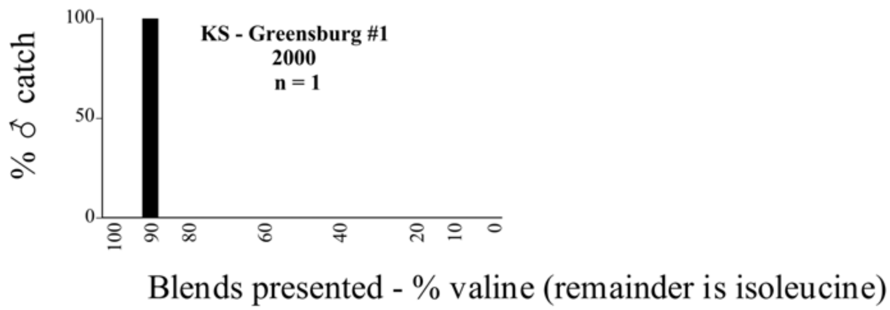


Figure 101 *P. lanceolata* ♂ catches

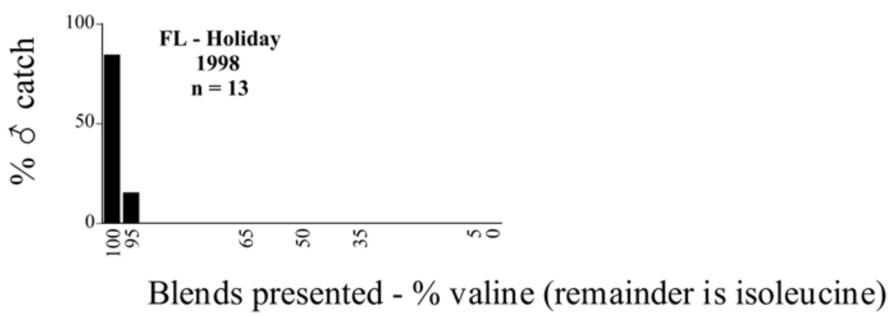


Figure 102 *P. latifrons* ♂ catches

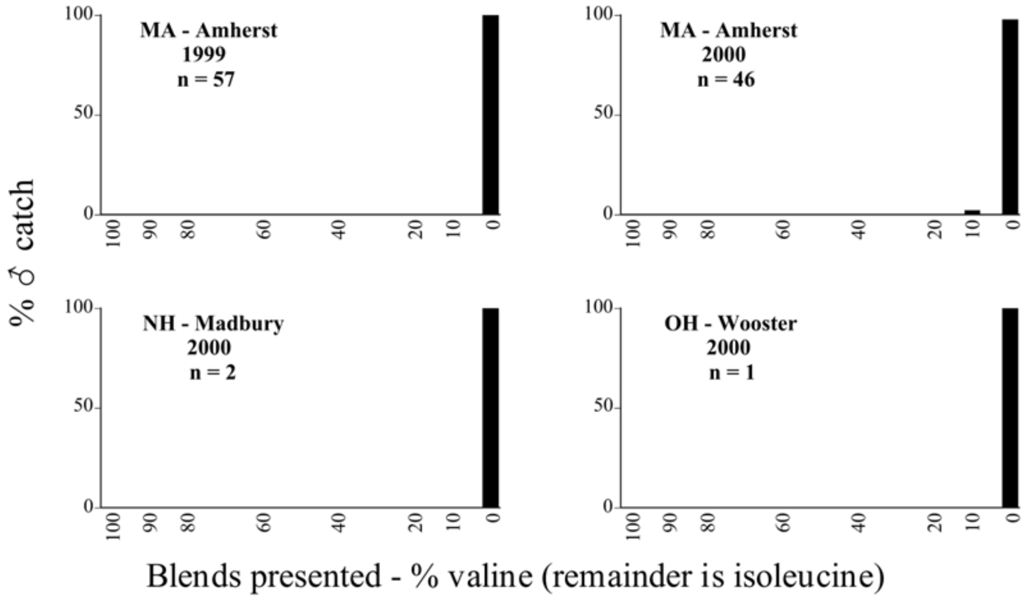


Figure 103 *P. longispina* ♂ catches

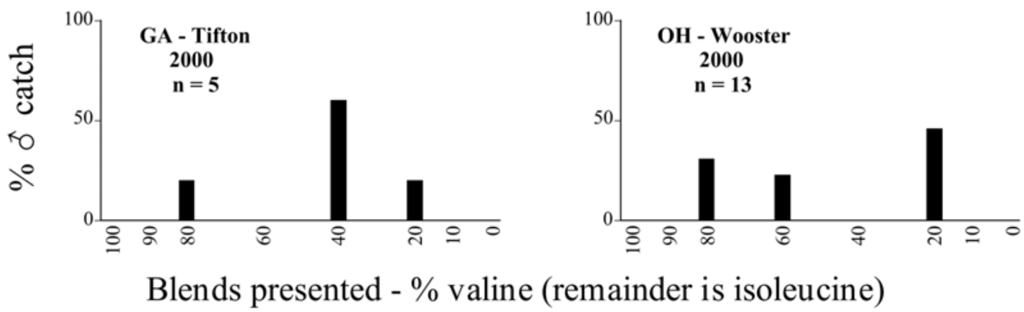


Figure 104 *lota* ♂ catches

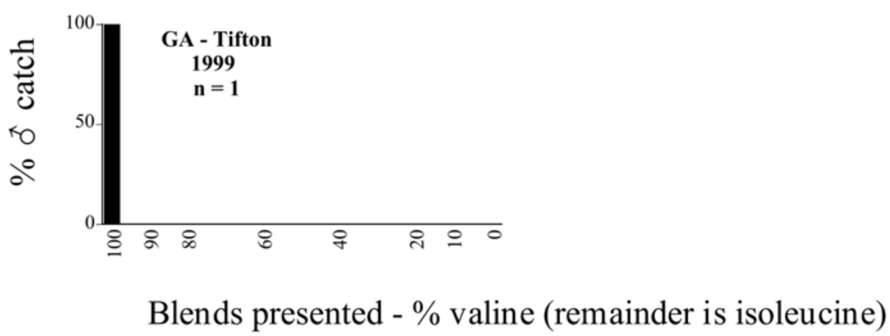


Figure 105 *P. luctuosa* ♂ catches

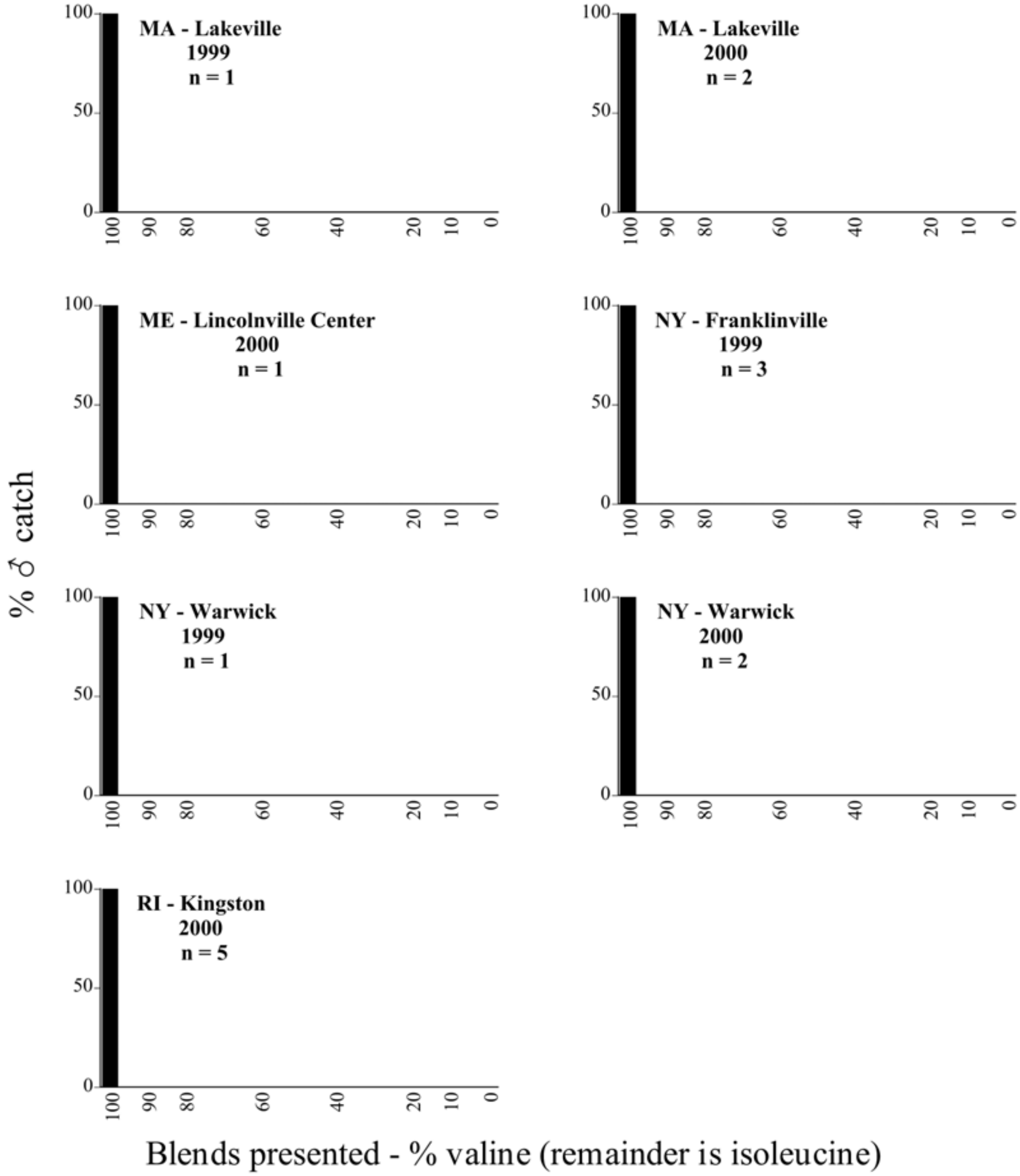


Figure 106 *P. marginalis* ♂ catches

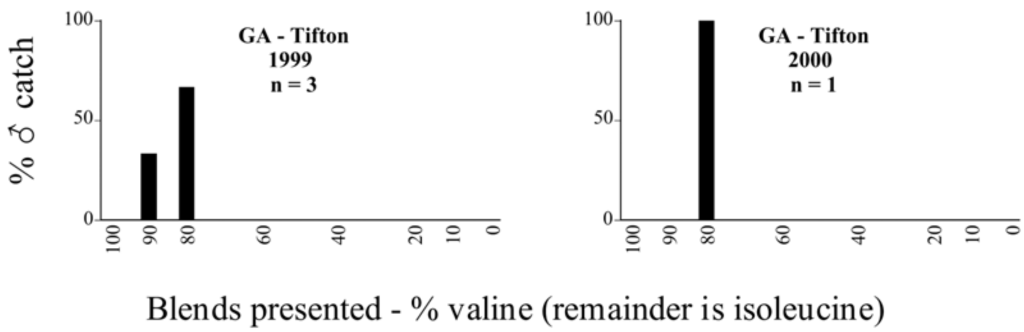


Figure 107 *P. mariana* ♂ catches

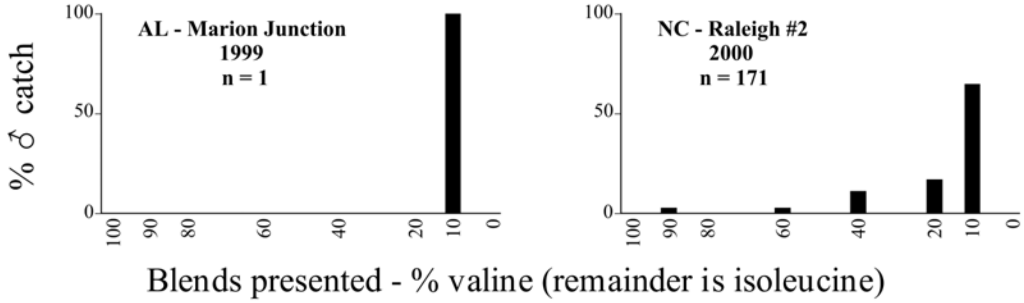


Figure 108 *P. micans* ♂ catches

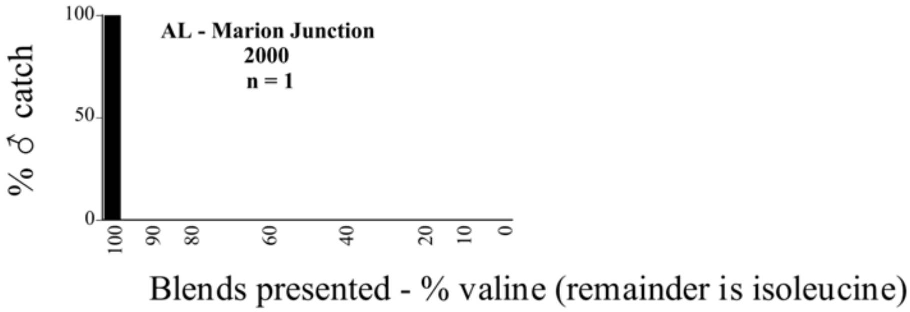


Figure 109 *P.* (*fraterna*) mississippiensis ♂ catches

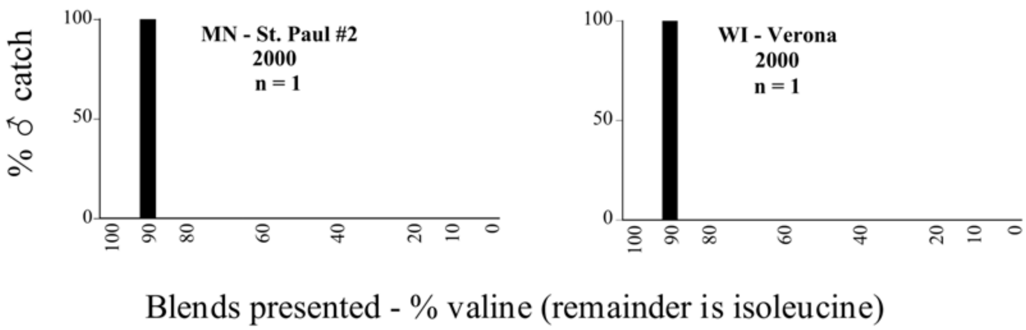


Figure 110 *P. nitida* ♂ catches

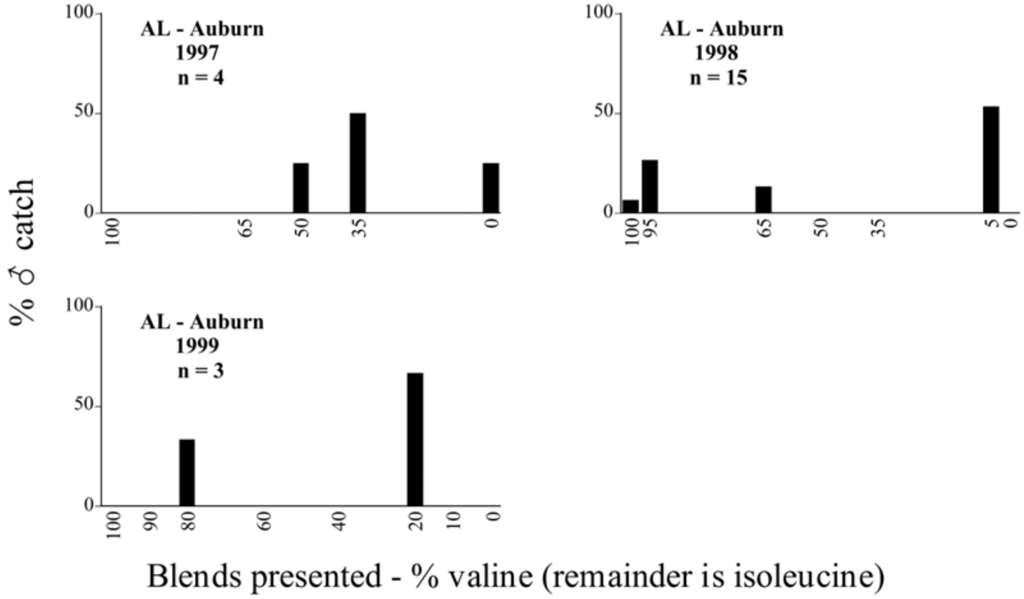


Figure 111 *P. obsoleta* ♂ catches

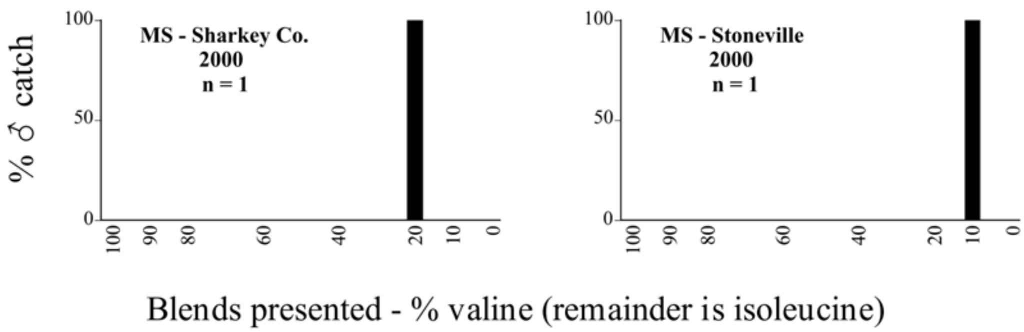


Figure 112 *P. perlonga* ♂ catches

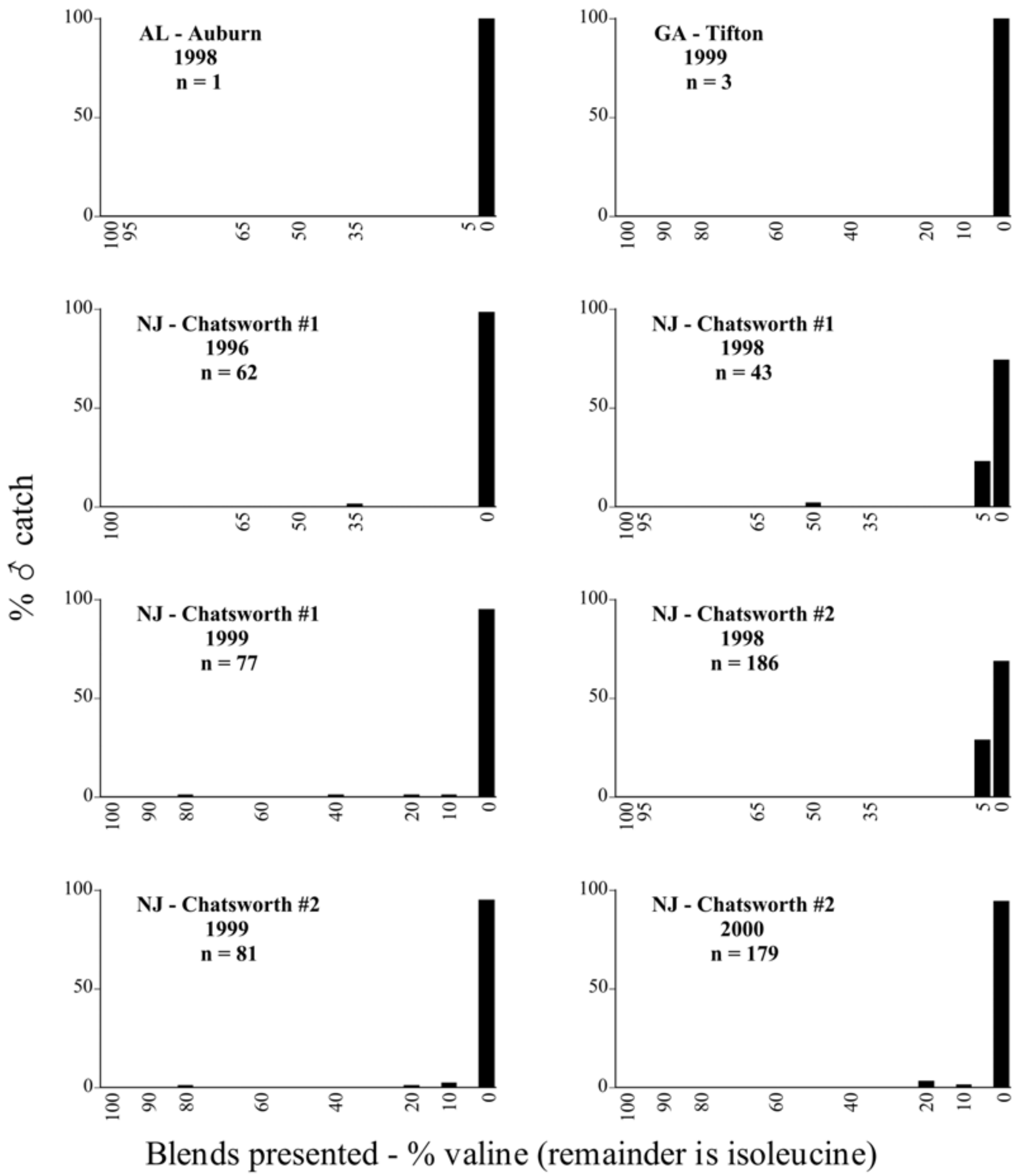


Figure 113 *P. postrema* ♂ catches

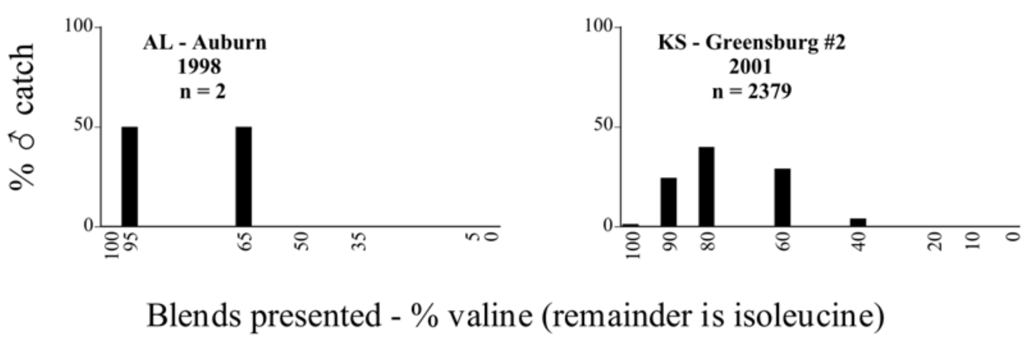


Figure 114 *P. praetermissa* ♂ catches

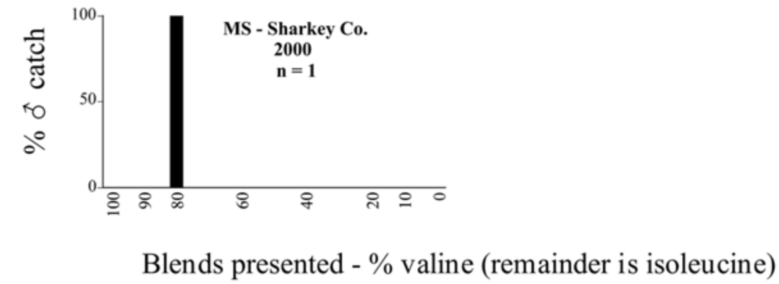


Figure 115 *P. profunda* ♂ catches

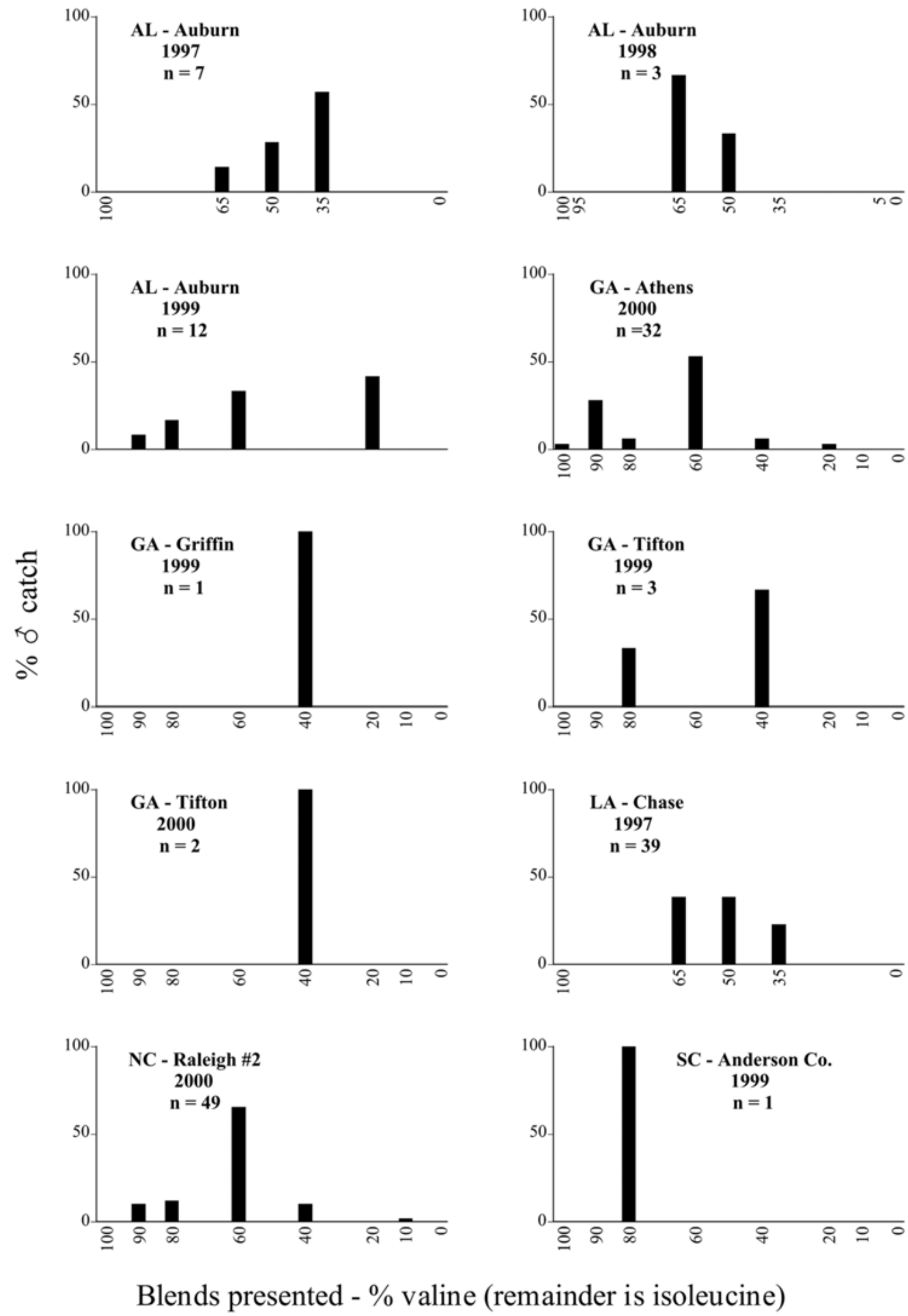


Figure 116 *P. quercus* ♂ catches

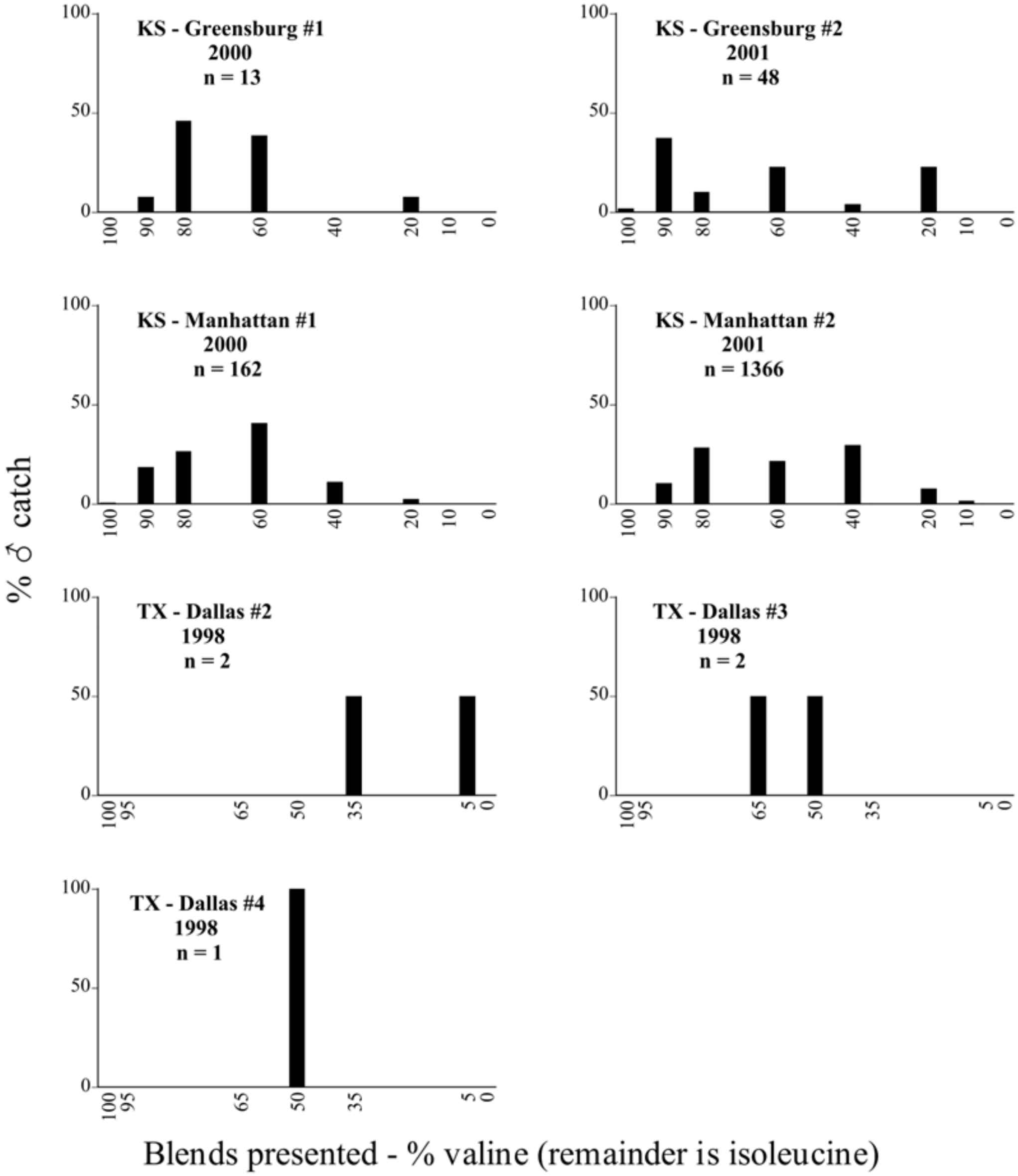


Figure 117 *P. rubiginosa* ♂ catches

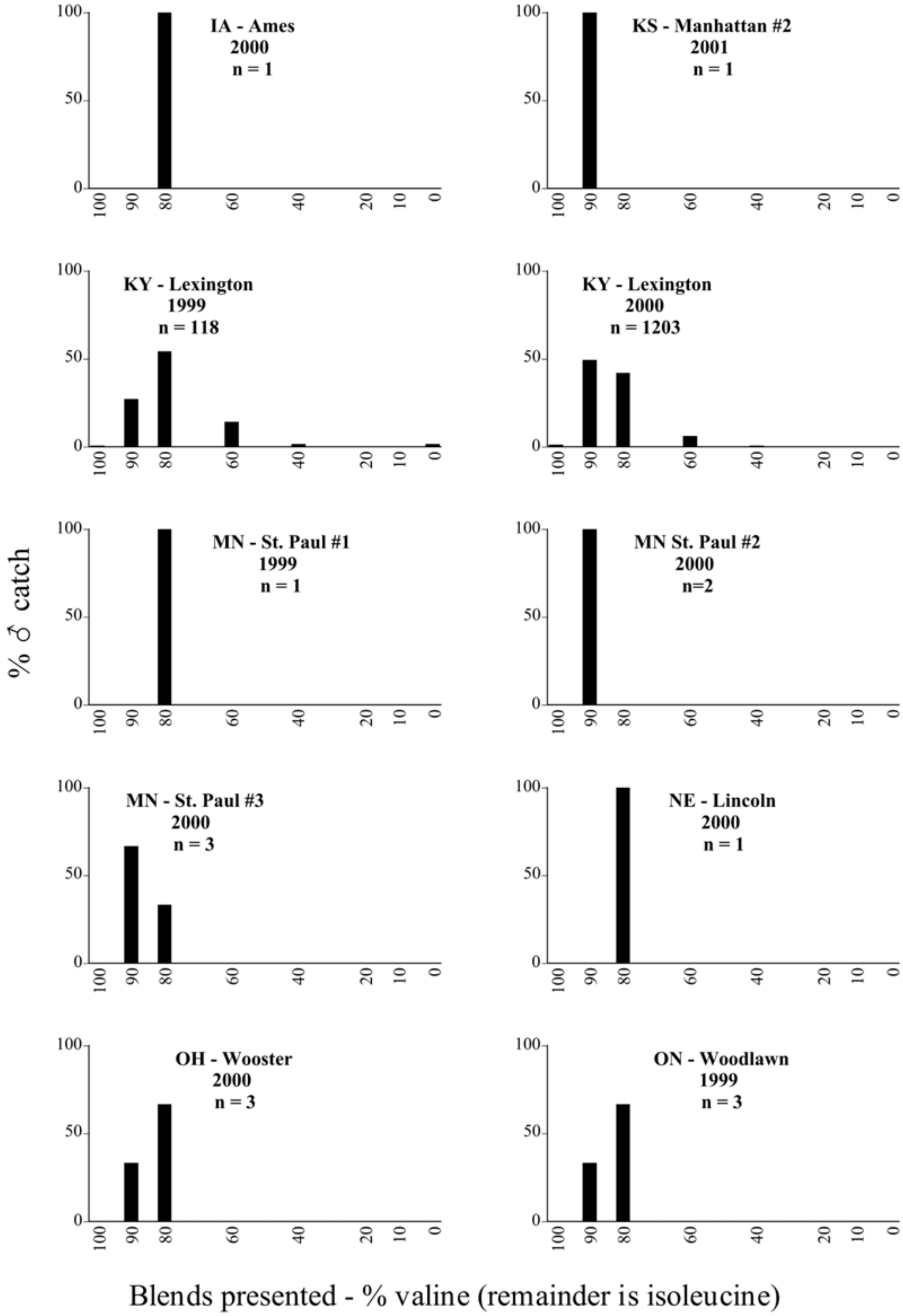


Figure 118a *P. rugosa* ♂ catches

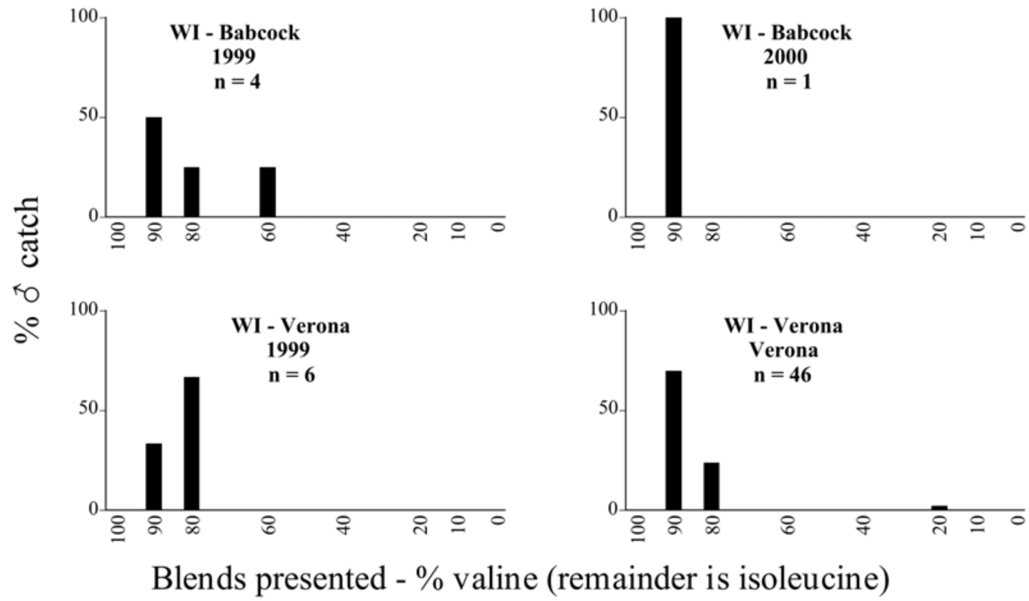


Figure 118b *P. rugosa* ♂ catches

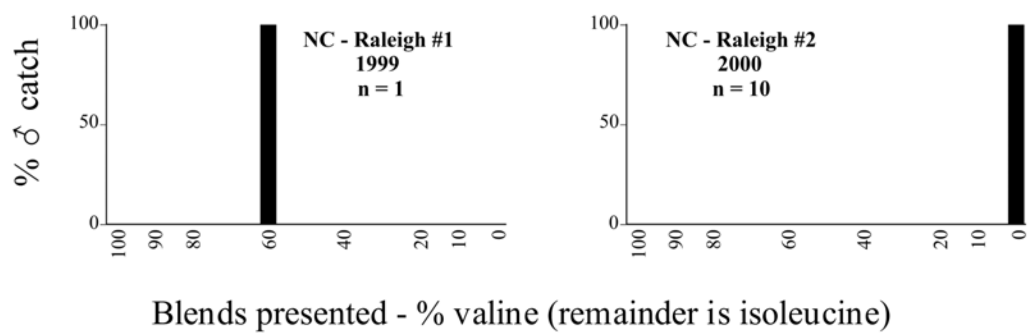


Figure 119 *P. soror* ♂ catches

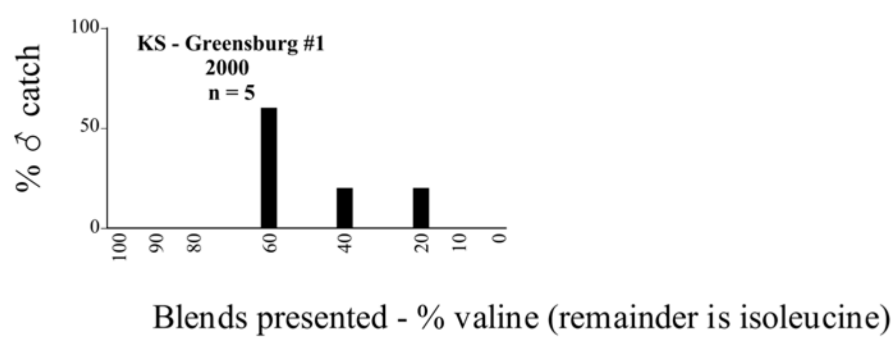


Figure 120 *P. submucida* ♂ catches

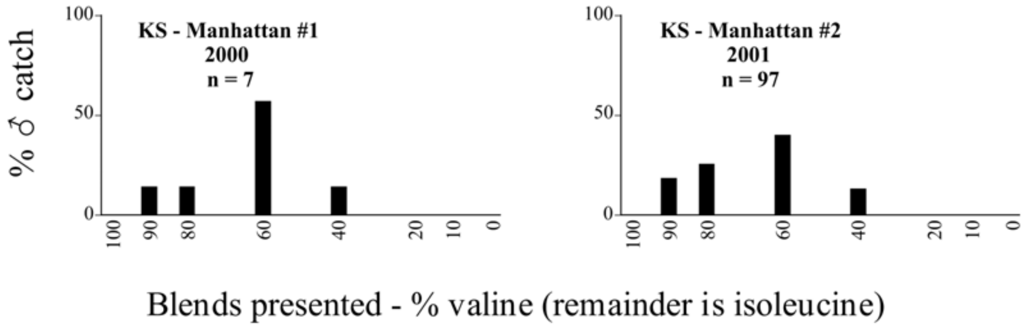


Figure 121 *P. sylvatica* ♂ catches

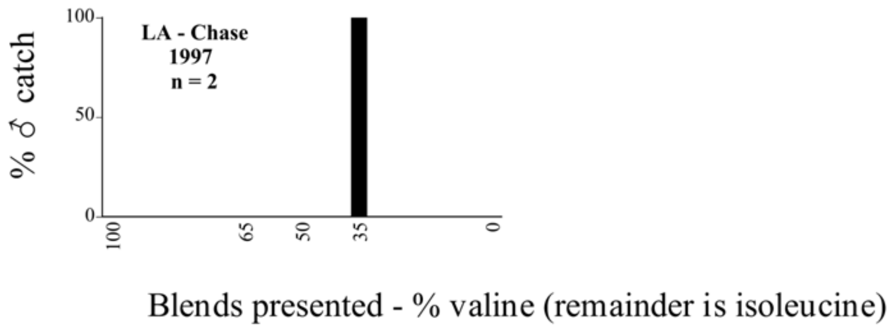


Figure 122 *P. taxodii* ♂ catches

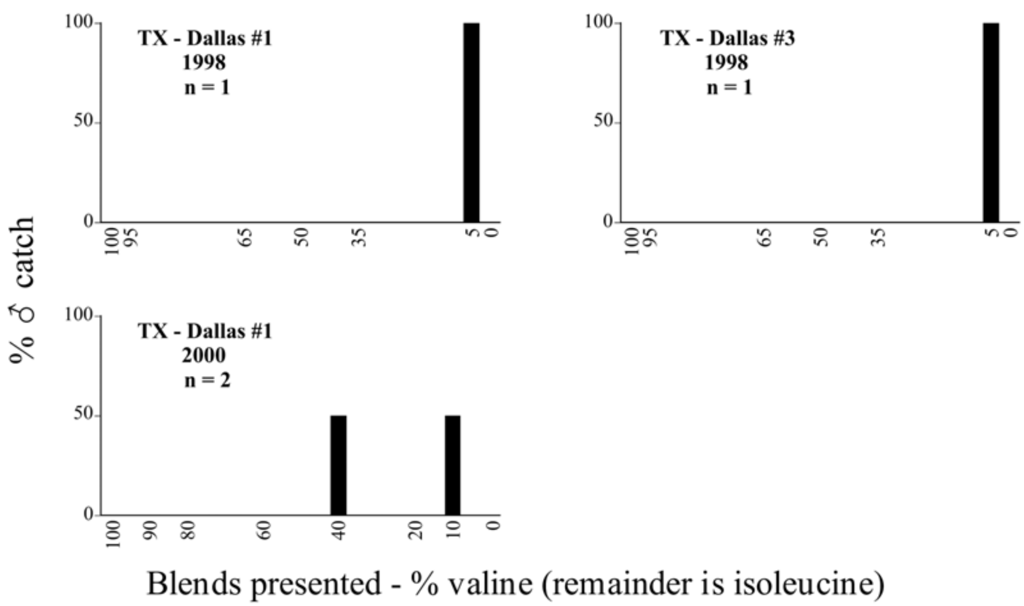


Figure 123 *torta* ♂ catches

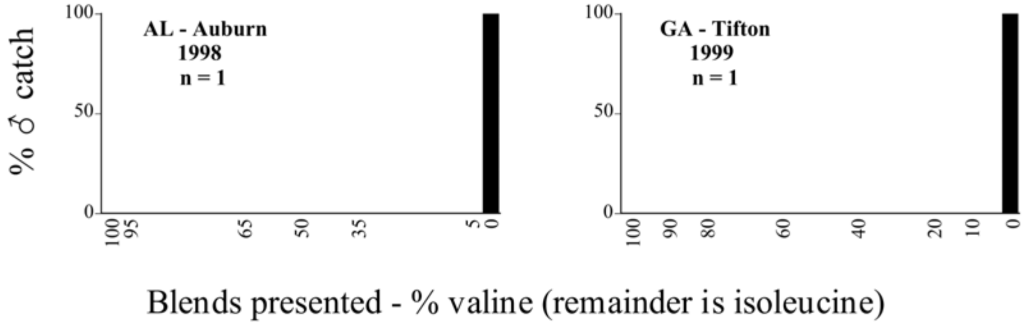


Figure 124 *P. ulkei* ♂ catches

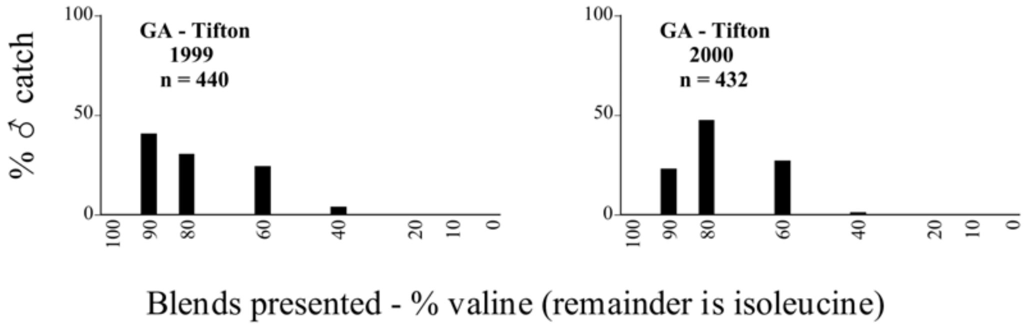


Figure 125 *P. uniformis* ♂ catches

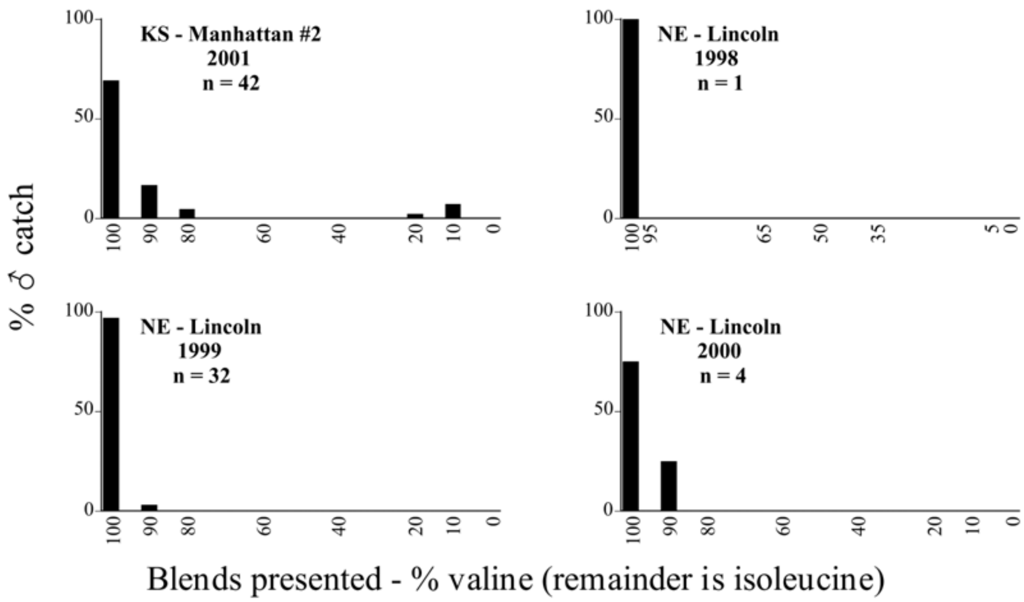


Figure 126 *P. vehemens* ♂ catches

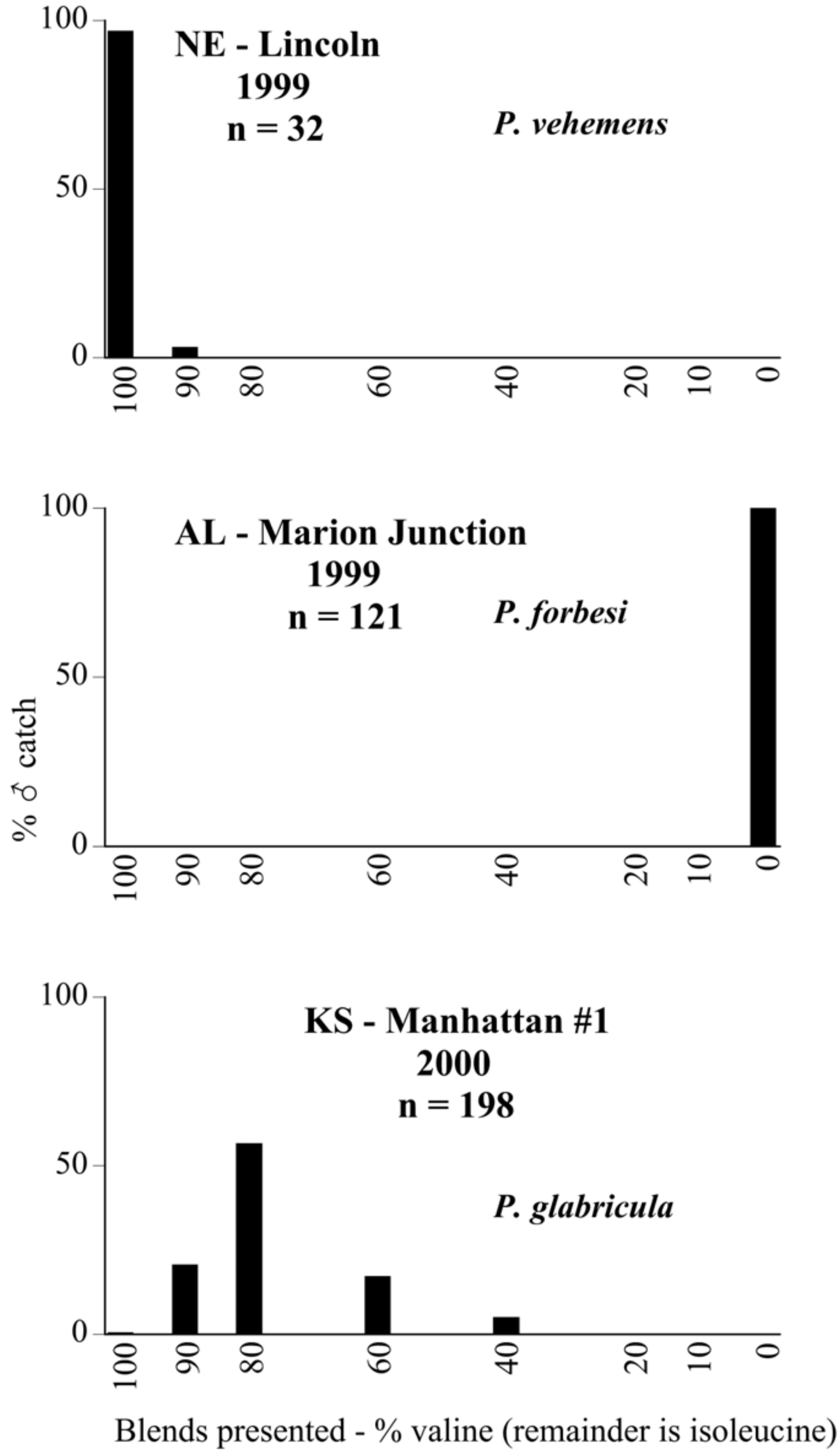
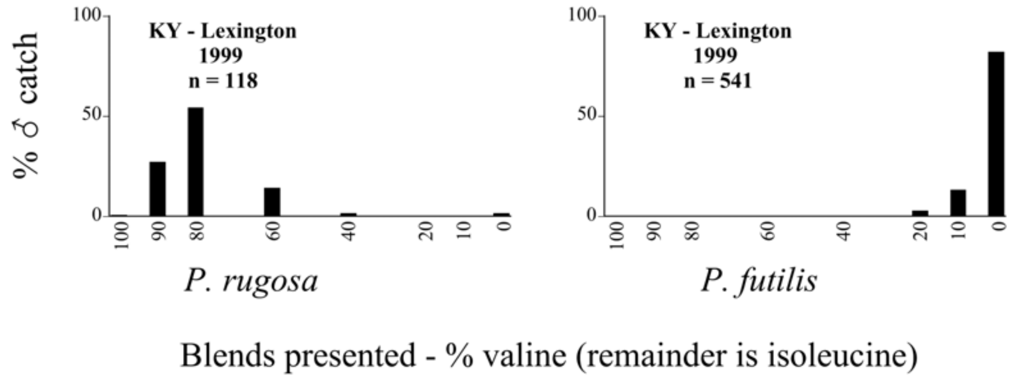
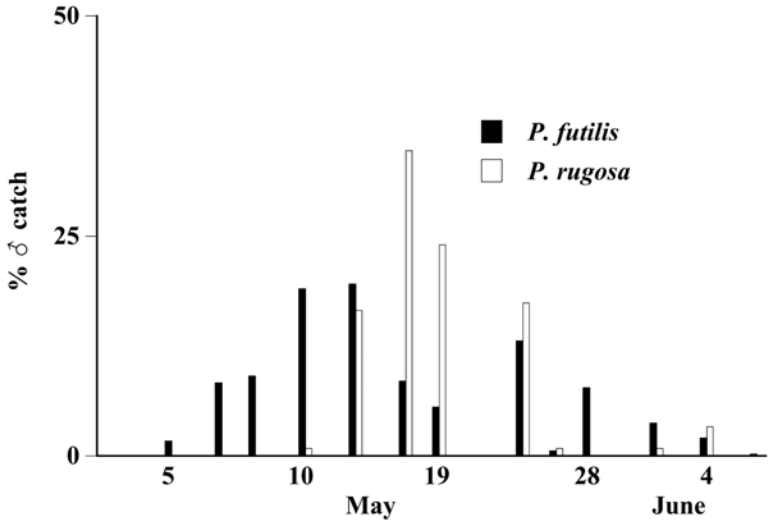


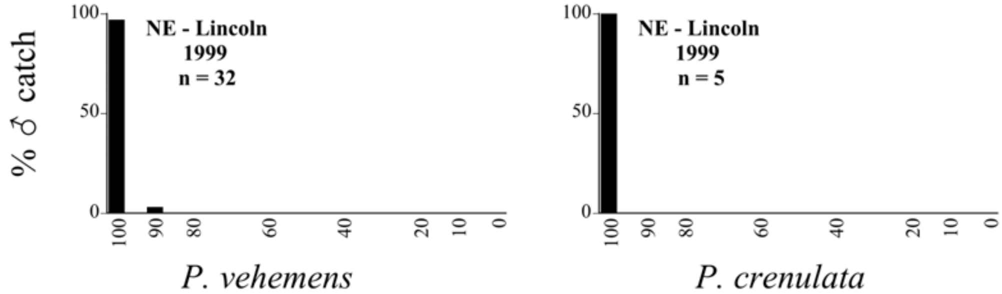
Figure 127 Response curves of ♂ *Phyllophaga* to sex attractants.



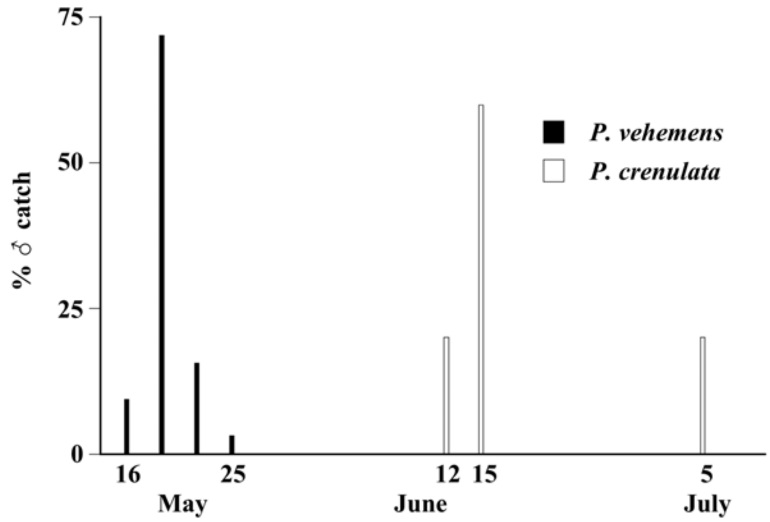


P. futilis and *P. rugosa* overlapping ♂ flight periods.

Figure 128 Sympatric *Phyllophaga* species flying synchronically to different blends of valine/isoleucine. Kentucky, Lexington, 1999.

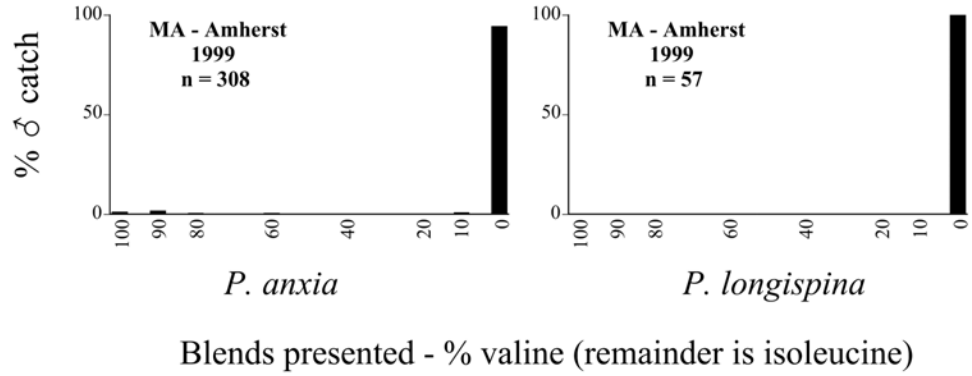


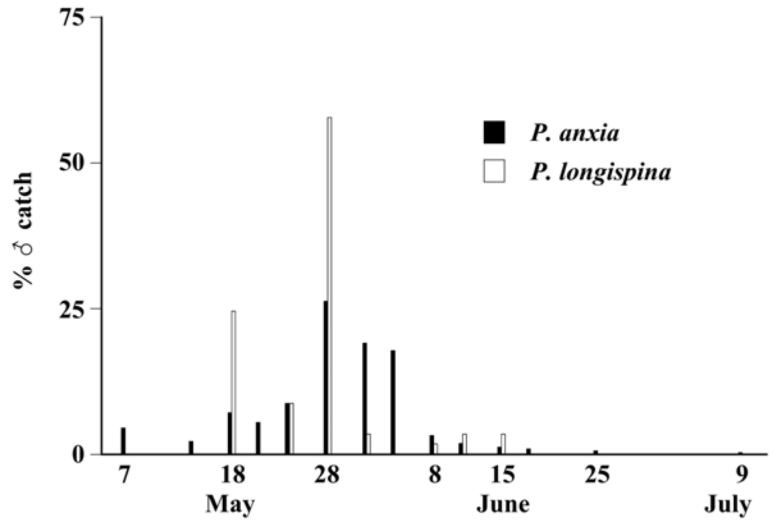
Blends presented - % valine (remainder is isoleucine)



P. vehemens and *P. crenulata*, non-overlapping ♂ flight periods.

Figure 129 Sympatric *Phyllophaga* species flying asynchronically to the same pheromone. Nebraska, Lincoln, 1999.





P. anxia and *P. longispina* overlapping ♂ flight periods.

Figure 130 Sympatric *Phyllophaga* species flying synchronically to the same pheromone. Massachusetts, South Amherst, 1999.

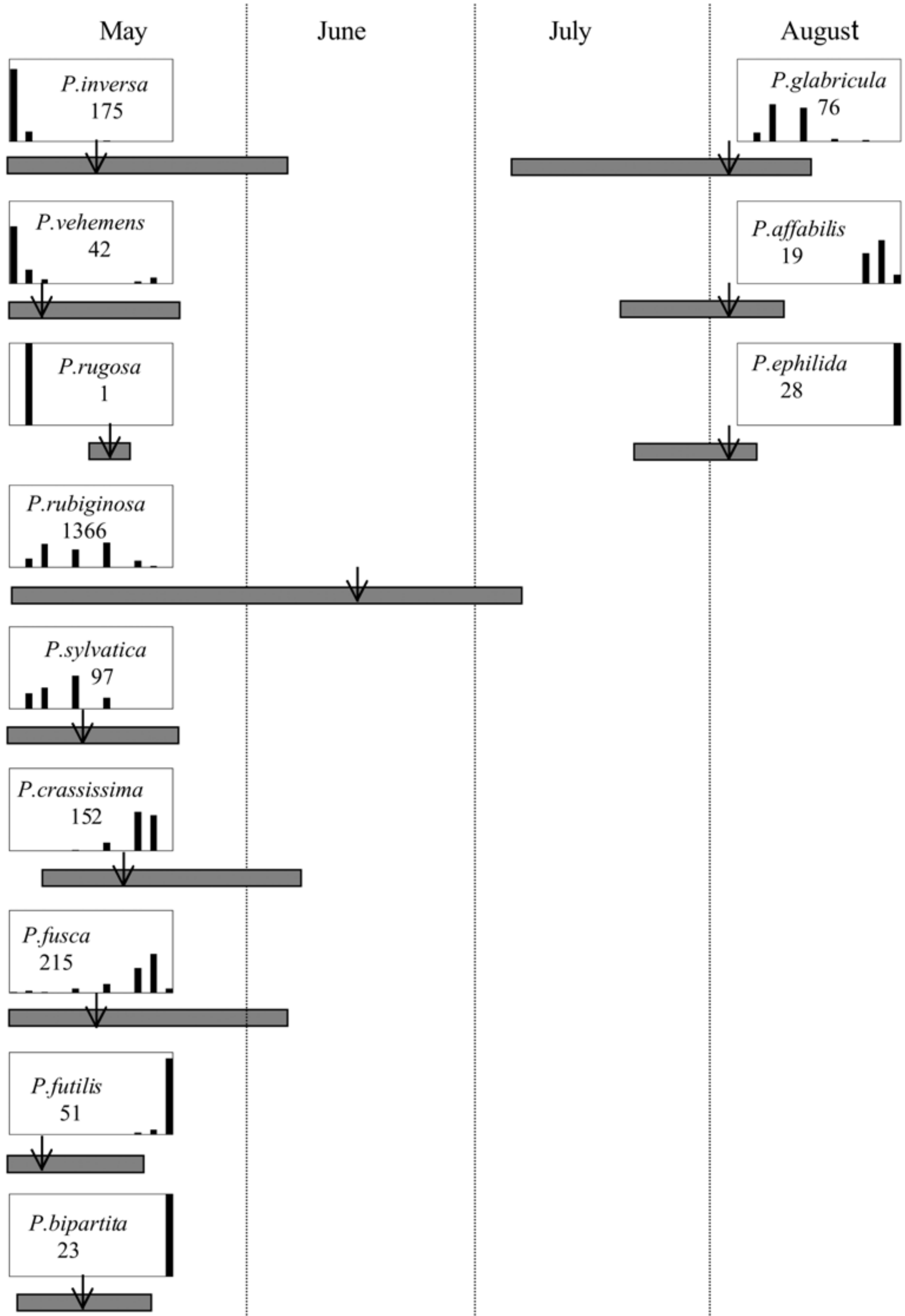


Figure 131 Kansas, Manhattan #2, 2001. Timing and duration of flight and ♂ pheromone response curves. Arrows indicate numerical midpoints of flights.

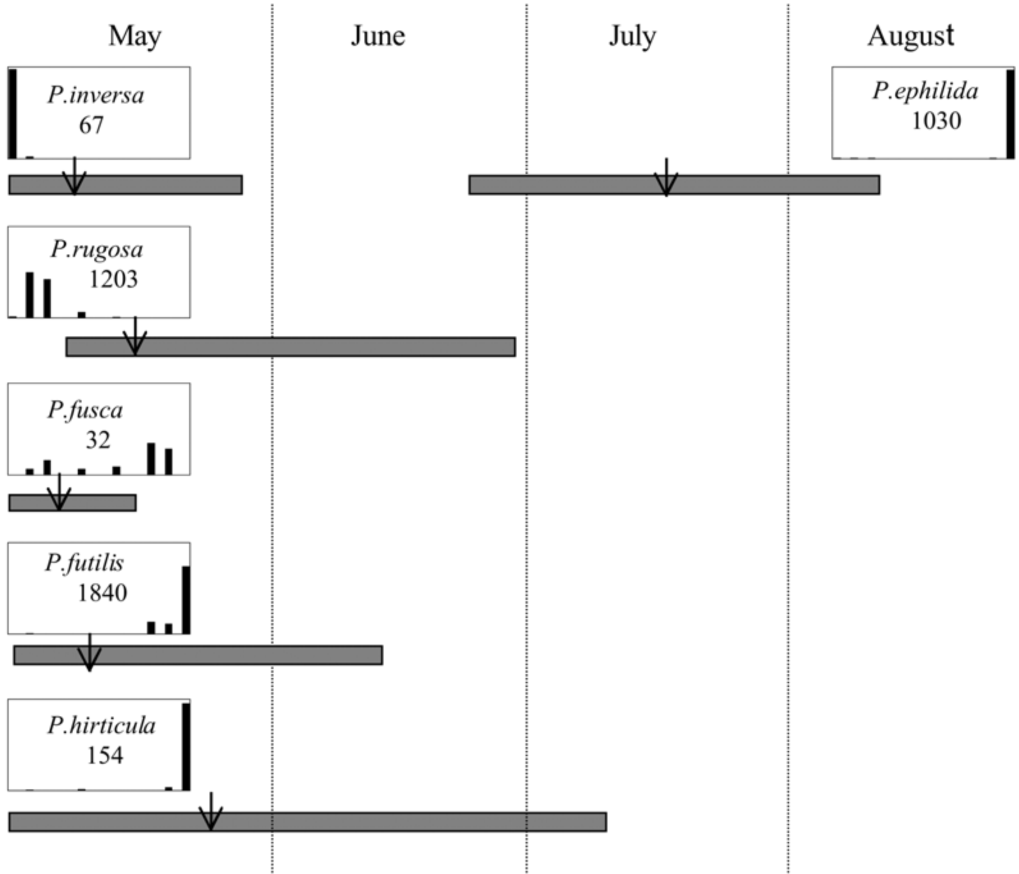


Figure 132 Kentucky, Lexington, 2000. Timing and duration of flight and ♂ pheromone response curves. Arrow indicates numerical midpoint of flight.

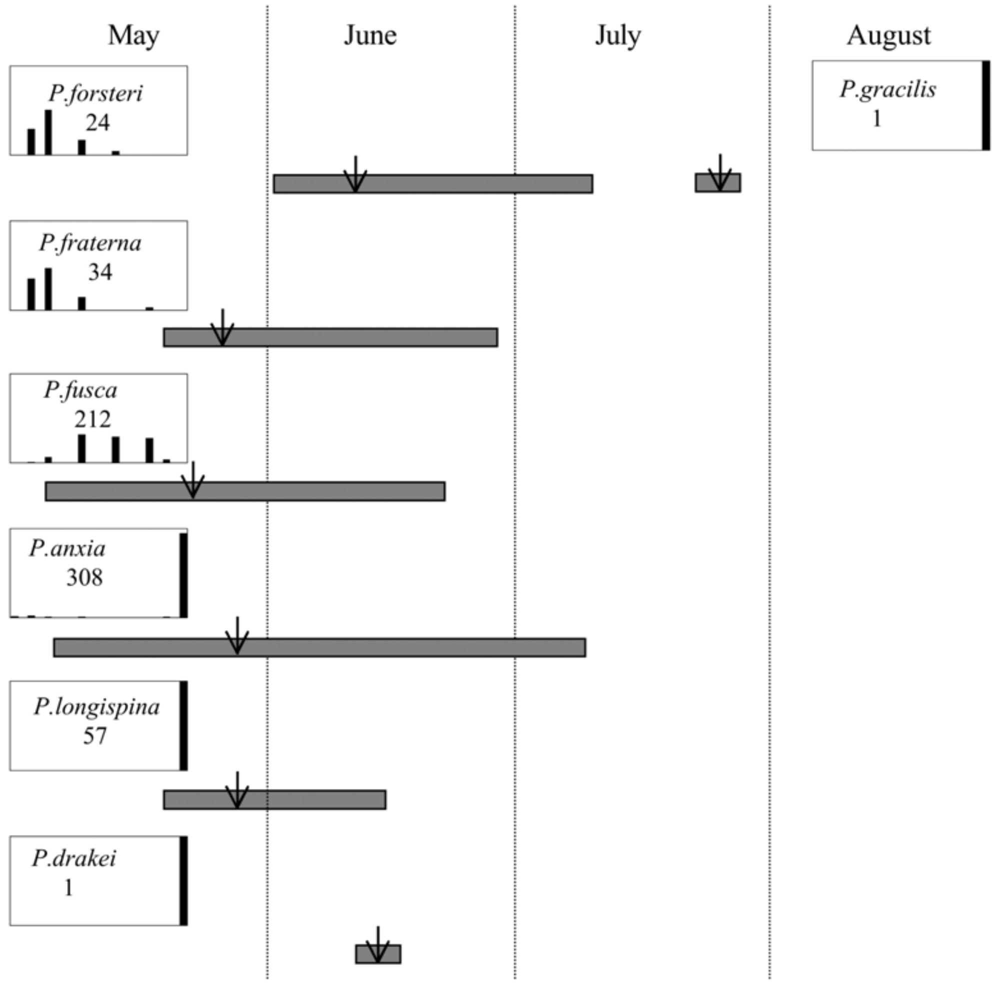


Figure 133 Massachusetts, Amherst, 1999. Timing and duration of flight and ♂ pheromone response curves. Arrow indicates numerical midpoint of flight.

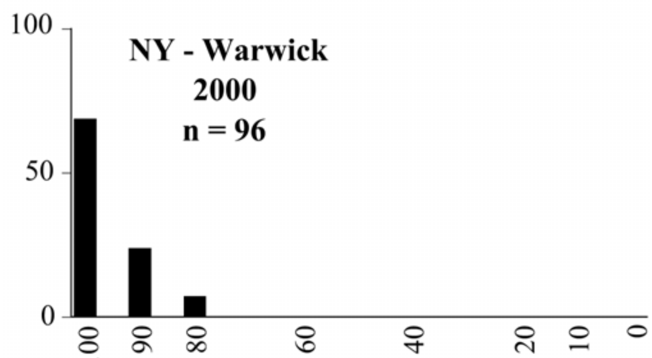


Figure 134 Valine responding ♂ capture curve, *P. anxia*.

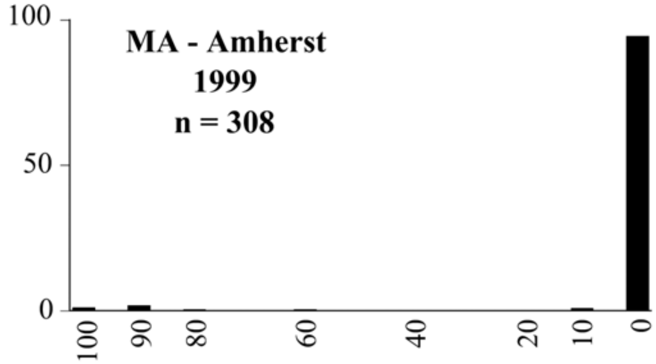


Figure 135 Isoleucine responding ♂ capture curve, *P. anxia*.

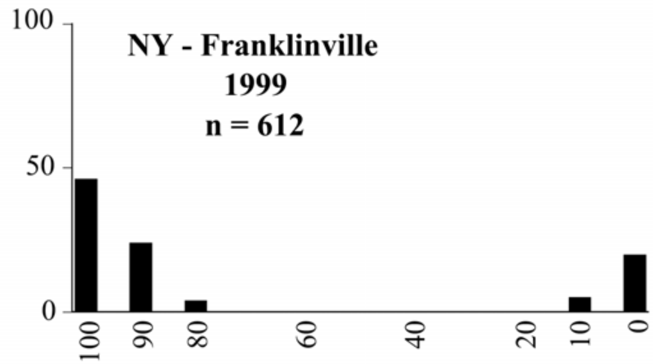


Figure 136 Bimodal ♂ capture curve, *P. anxia*.

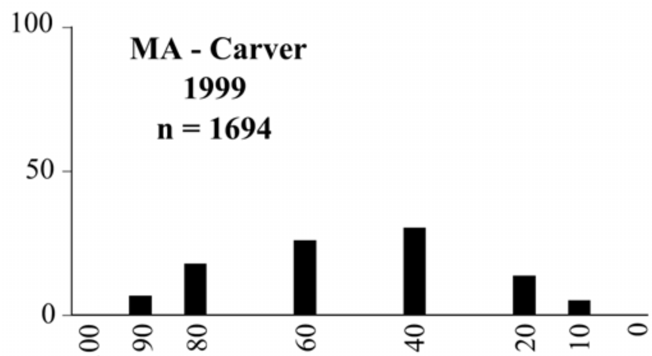


Figure 137 Blend responding ♂ capture curve, *P. anxia*.

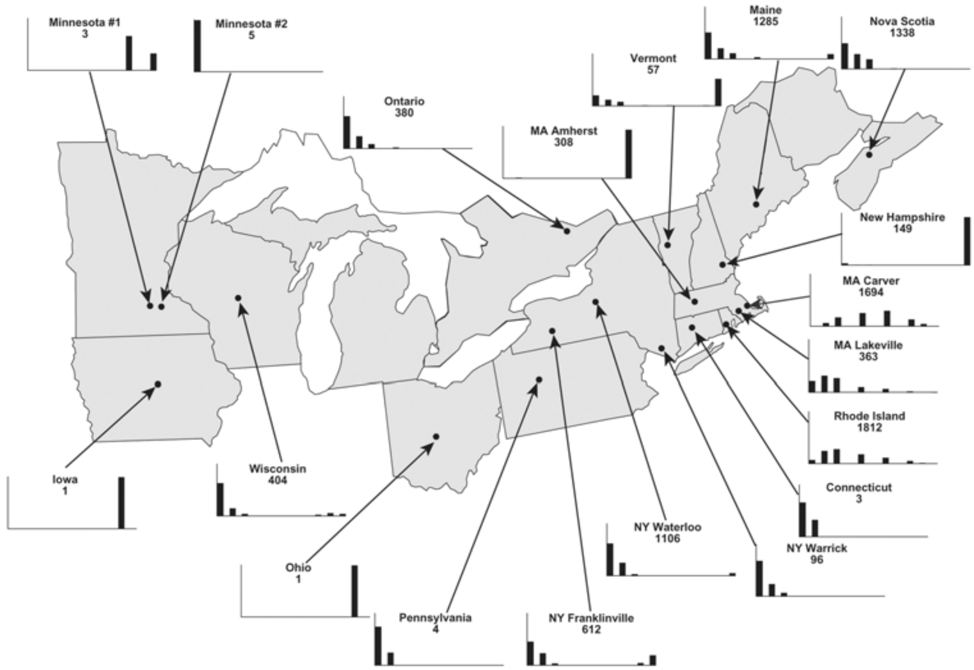


Figure 138 ♂ capture curves for *Phyllophaga anxia* (LeConte), northern genitalic form (n = 20,460. Not all locations shown in this figure.)

Tables

Table 1a.

State or Province	City	Years	Habitat/Trap Placement
Alabama	Auburn	97,98,99	sparse pecan grove
Alabama	Marion Junction (research farm)	99,00	research farm, edge of woods
British Columbia	Aggasiz	99	cranberry bog
Connecticut	Vernon	99, 00	suburban
Florida	Holiday	98	edge of wooded suburban area
Florida	Homestead (research farm)	00	suburban
Georgia	Athens	99,00	Athens Botanical Gardens
Georgia	Griffin	99	rural farmland/pasture
Georgia	Tifton	99,00	rural farmland/pasture
Indiana	West Lafayette	2000	suburban - mixed trees and non-maintained turf
Iowa	Ames	99,00	grassy area at edge of woods
Kansas	Greensburg #1	00	mixed grass range land
Kansas	Greensburg #2	01	mixed grass range land
Kansas	Manhattan #1	00	golf course
Kansas	Manhattan #2	01	golf course
Kentucky	Lexington (research farm)	99,00	tall fescue pasture next to tree nursery plantings
Louisiana	Chase (research farm)	97, 98	near tree line at the edge of a sweet potato field
Maine	Lincolnville Center	99,00	small cranberry bog surrounded by woods
Massachusetts	South Amherst	99,00	suburban, edge of woods near horse pasture
Massachusetts	Carver	96,98,99,00	large cranberry bog
Massachusetts	Lakeville	99,00	cranberry bog near woods
Massachusetts	Plympton #1	96	small cranberry bog surrounded by woods
Massachusetts	Plympton #2	96	small cranberry bog surrounded by woods
Minnesota	St. Paul #1	99	golf course
Minnesota	St. Paul #2	00	golf course
Minnesota	St. Paul #3	00	golf course
Mississippi	Leroy Percy State Park	00	treeline near grass/weed field
Mississippi	Sharkey Co., 7 miles SE of Anguilla	00	treeline near grass/weed field
Mississippi	Stoneville	00	treeline near grass/weed field
Nebraska	Lincoln	98,99,00	suburban

Table 1b.

State or Province	City	Years	Habitat/Trap Placement
New Hampshire	Madbury (research farm)	99, 00	pasture grasses surrounded by woods
New Jersey	Chatsworth #1	96,98,99	cranberry bog
New Jersey	Chatsworth #2	98,99,00	cranberry bog
New Jersey	Hammonton	96	commercial blueberry planting
New Jersey	New Brunswick	99	edge of woods near horse pasture and vegetables
New York	Bellona	98,99,00	edge of woods adjacent to farm land
New York	Franklinville	99	edge of woods adjacent to grassy area
New York	Riverhead	99	suburban
New York	Saratoga Springs	99,00	New York State Tree Nursery
New York	Warwick	99,00	golf course
New York	Waterloo #1	98,99,00	edge of woods adjacent to grassy area
New York	Waterloo #2	98	edge of woods adjacent to grassy area
North Carolina	Raleigh #1 (turfgrass research farm)	99	near tall fescue planting
North Carolina	Raleigh #2	0	rural subdivision– 50/50 mix of trees and turf
Nova Scotia	Kentville Center (research farm)	99,00	edge of woods near pasture, apple orchards
Ohio	Columbus (research farm)	0	turfgrass research farm at edge of woods
Ohio	Wooster (research farm)	0	edge of woods adjacent to grassy area
Ontario	Woodlawn	99,00	edge of cedar/balsam forest near marshy field
Oregon	Bandon	99	cranberry bog near woods
Pennsylvania	State College (research farm)	99,00	edge of woods adjacent to grassy area
Rhode Island	Kingston	99,00	commercial azalea nursery
South Carolina	Anderson Co. (research farm).	99	fence line between orchard and pasture near woods
Texas	Dallas #1 (research farm)	98,99,00	fence line dividing forage pasture/turf plots
Texas	Dallas #2 (research farm)	98	edge of oak tree nursery with weedy undergrowth
Texas	Dallas #3 (research farm)	98	edge of mixed wild grasses
Texas	Dallas #4 (research farm)	98	edge of mixed wild grasses
Utah	Salt Lake City (Red Butte Canyon)	99	grassland/forb community
Vermont	Burlington	99,00	grass area near woods
Wisconsin	Babcock	99,00	large cranberry bog
Wisconsin	Verona (turfgrass research farm)	99,00	wooded fencerow near non-maintained grassy area

Table 2a. Male catches, sites, and sites-years sorted by species.

***Phyllophaga* species**	**n**	**sites**	**site-years**
aemula	231	1	2
affabilis	77	1	2
anxia TOTAL	20480	33	54
anxia NORTHERN	20460	25	45
anxia SOUTHERN	20	8	9
balia	5	3	4
bipartita	38	2	2
clypeata	2	1	1
congrua	6916	8	10
corrosa	59	2	2
crassissima	5710	11	15
crenulata	15	5	7
crinita	24	7	9
curialis	1	1	1
davisi	6	1	1
diffinis	2	1	1
drakei	91	11	18
ephilida	1726	12	15
fervida	3	1	1
forbesi	141	2	3
forsteri	141	16	26
foxii	1	1	1
fraterna	111	8	14
fraterna-like	37	1	2
fusca	1040	21	37
futilis	7575	20	32
georgiana	2	1	1
glaberrima	70	2	3
glabricula	274	1	2
gracilis	1930	4	7
gracilis var. *angulata*	6	2	2
hirsuta	2	2	2
hirticula	191	5	7
hirtiventris	1820	7	8
ilicis	1	1	1
implicita	3	2	2
inversa	452	5	8

Table 2b. Male catches, sites, and sites-years sorted by species.

***Phyllophaga* species**	**n**	**sites**	**site-years**
kentuckiana	1	1	1
lanceolata	1	1	1
latifrons	13	1	1
longispina	106	3	4
lota	18	2	2
luctuosa	1	1	1
marginalis	15	5	7
mariana	4	1	2
micans	172	2	2
mississippiensis	1	1	1
nitida	2	2	2
obsoleta	22	1	3
perlonga	2	2	2
postrema	632	4	8
praetermissa	2381	2	2
profunda	1	1	1
quercus	149	7	10
rubiginosa	1594	7	7
rugosa	1393	11	14
soror	11	2	2
submucida	5	1	1
sylvatica	104	2	2
taxodii	2	1	1
torta	4	3	3
ulkei	2	2	2
uniformis	872	1	2
vehemens	79	2	4

Table 3a. Male catches, sites, and sites-years sorted by n.

***Phyllophaga* species**	**n**	**sites**	**site-years**
anxia TOTAL	20480	33	54
anxia NORTHERN	20460	25	45
futilis	7575	20	32
congrua	6916	8	10
crassissima	5710	11	15
praetermissa	2381	2	2
gracilis	1930	4	7
hirtiventris	1820	7	8
ephilida	1726	12	15
rubiginosa	1594	7	7
rugosa	1393	11	14
fusca	1040	21	37
uniformis	872	1	2
postrema	632	4	8
inversa	452	5	8
glabricula	274	1	2
aemula	231	1	2
hirticula	191	5	7
micans	172	2	2
quercus	149	7	10
forbesi	141	2	3
forsteri	141	16	26
fraterna	111	8	14
longispina	106	3	4
sylvatica	104	2	2
drakei	91	11	18
vehemens	79	2	4
affabilis	77	1	2
glaberrima	70	2	3
corrosa	59	2	2
bipartita	38	2	2
fraterna-like	37	1	2
crinita	24	7	9
obsoleta	22	1	3
anxia SOUTHERN	20	8	9
lota	18	2	2
crenulata	15	5	7

Table 3b. Male catches, sites, and sites-years sorted by n.

***Phyllophaga* species**	**n**	**sites**	**site-years**
marginalis	15	5	7
latifrons	13	1	1
soror	11	2	2
davisi	6	1	1
gracilis var. *angulata*	6	2	2
balia	5	3	4
submucida	5	1	1
mariana	4	1	2
torta	4	3	3
fervida	3	1	1
implicita	3	2	2
clypeata	2	1	1
diffinis	2	1	1
georgiana	2	1	1
hirsuta	2	2	2
nitida	2	2	2
perlonga	2	2	2
taxodii	2	1	1
ulkei	2	2	2
curialis	1	1	1
foxii	1	1	1
ilicis	1	1	1
kentuckiana	1	1	1
lanceolata	1	1	1
luctuosa	1	1	1
mississippiensis	1	1	1
profunda	1	1	1

Table 4a. Male catches, sites, and sites-years sorted by sites.

***Phyllophaga* species**	**n**	**sites**	**site-years**
anxia TOTAL	20480	33	54
anxia NORTHERN	20460	25	45
fusca	1040	21	37
futilis	7575	20	32
forsteri	141	16	26
ephilida	1726	12	15
crassissima	5710	11	15
rugosa	1393	11	14
drakei	91	11	18
congrua	6916	8	10
fraterna	111	8	14
anxia SOUTHERN	20	8	9
hirtiventris	1820	7	8
rubiginosa	1594	7	7
quercus	149	7	10
crinita	24	7	9
inversa	452	5	8
hirticula	191	5	7
crenulata	15	5	7
marginalis	15	5	7
gracilis	1930	4	7
postrema	632	4	8
longispina	106	3	4
balia	5	3	4
torta	4	3	3
praetermissa	2381	2	2
micans	172	2	2
forbesi	141	2	3
sylvatica	104	2	2
vehemens	79	2	4
glaberrima	70	2	3
corrosa	59	2	2
bipartita	38	2	2
lota	18	2	2
soror	11	2	2
gracilis var. *angulata*	6	2	2
implicita	3	2	2

Table 4b. Male catches, sites, and sites-years sorted by sites.

***Phyllophaga* species**	**n**	**sites**	**site-years**
hirsuta	2	2	2
nitida	2	2	2
perlonga	2	2	2
ulkei	2	2	2
uniformis	872	1	2
glabricula	274	1	2
aemula	231	1	2
affabilis	77	1	2
fraterna-like	37	1	2
obsoleta	22	1	3
latifrons	13	1	1
davisi	6	1	1
submucida	5	1	1
mariana	4	1	2
fervida	3	1	1
clypeata	2	1	1
diffinis	2	1	1
georgiana	2	1	1
taxodii	2	1	1
curialis	1	1	1
foxii	1	1	1
ilicis	1	1	1
kentuckiana	1	1	1
lanceolata	1	1	1
luctuosa	1	1	1
mississippiensis	1	1	1
profunda	1	1	1

Table 5. Alabama, Auburn 1997
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. forsteri ♂	1	1				
P. gracilis ♂	14	8	10	13	1068	10
P. hirticula ♂					1	
P. obsoleta ♂			1	2	1	7
P. quercus ♂		1	2	4		
*P.*near *fraterna* ♂			1			
P. gracilis ♀	1		3	2	2	3
P. obsoleta ♀	1		1	1		1
P. quercus ♀	1				1	

A total of 1163 *Phyllophaga* were taken between 6/9/97 and 8/22/97.

Table 6. Alabama, Auburn 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. anxia ♂							1	
P. crinita ♂					1			
P. diffinis ♂	2							
P. forsteri ♂	2	8						
P. gracilis ♂	3	9	1	1	14	214	464	4
P. hirticula ♂	2	2					26	1
P. obsoleta ♂	1	4	2			8		13
P. postrema ♂							1	
P. praetermissa ♂		1	1					
P. quercus ♂			2	1				
P. ulkei ♂							1	
P. gracilis ♀			1	1		1	1	1
P. hirticula ♀					1		1	
P. obsoleta ♀		1	1		1	4	2	1
P. ulkei ♀	1							

A total of 808 *Phyllophaga* were taken between 3/30/98 and 8/11/98.

Table 7. Alabama, Auburn 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. forsteri ♂		4	6	2					
P. gracilis ♂	2	1	5	2	2	6	19	57	4
P. hirticula ♂					1				
P. obsoleta ♂			1			2			1
P. quercus ♂		1	2	4		5			
P. gracilis ♀	3				1				2
P. obsoleta ♀							3	1	1
P. quercus ♀									

A total of 140 *Phyllophaga* were taken between 4/12/99 and 8/17/99.

Table 8. Alabama, Marion Junction 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. crenulata ♂	3								
P. davisi ♂								6	
P. forbesi ♂								121	1
P. futilis ♂								1	
P. hirtiventris ♂	23	2	2						
P. micans ♂							1		

A total of 160 *Phyllophaga* were taken between 4/5/99 and 7/26/99.

Table 9. Alabama, Marion Junction 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. crinita ♂	1						4		
P. forbesi ♂								10	
P. gracilis angulata ♂								1	
P. hirtiventris ♂	19	14	3						
P. mississippiensis ♂	1								
P. crinita ♀	1								
P. forbesi ♀			1		2				
P. mississippiensis ♀								1	

A total of 56 *Phyllophaga* were taken between 5/19/00 and 8/16/00.

Table 10. Canada, Nova Scotia, Kentville Center 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	465	407	385	32	1				3
P. drakei ♂								10	
P. futilis ♂								1	

A total of 1304 *Phyllophaga* were taken between 5/10/99 and 7/2/99.

Table 11. Canada, Nova Scotia, Kentville Center 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	668	388	256	25	1				
P. drakei ♂								32	
P. anxia ♀			1						

A total of 1371 *Phyllophaga* were taken between 5/22/00 and 7/24/00.

Table 12. Canada, Ontario, Woodlawn 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	240	93	35	11	1				1
P. drakei ♂								1	
P. fusca ♂				1	1				
P. futilis ♂	2	1	1	2	4	6	14	71	1
P. rugosa ♂		1	2						

A total of 489 *Phyllophaga* were taken between 5/15/99 and 6/18/99.

Table 13. Canada, Ontario, Woodlawn 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	123	80	35	7	3				
P. drakei ♂								1	
P. fusca ♂				1	1				
P. futilis ♂		1	1			1	11	38	

A total of 303 *Phyllophaga* were taken between 5/4/00 and 7/7/00.

Table 14. Connecticut, Vernon 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	2	1							
P. forsteri ♂		2	2	1					
P. fraterna ♂		2	6	1					
P. fusca ♂		2		7	6	1			
P. hirticula ♂								3	

A total of 36 *Phyllophaga* were taken between 5/22/99 and 7/3/99.

Table 15. Connecticut, Vernon 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. forsteri ♂		1		1					
P. fraterna ♂		1							
P. fusca ♂				1					

A total of 4 *Phyllophaga* were taken on 6/20/00.

Table 16. Florida, Holiday 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. glaberrima ♂		6	14	4	12	3		
P. latifrons ♂	11	2						

A total of 52 Phyllophaga were taken between 4/22/98 and 7/16/98.

Table 17. Georgia, Athens 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. aemula ♂	16	48	18	1	1			1	
P. ephilida ♂								6	
P. forsteri ♂				1					

A total of 93 *Phyllophaga* were taken between 5/28/99 and 9/20/99.

Table 18. Georgia, Athens 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. aemula ♂	21	96	23	4	1				
P. anxia ♂								1	
P. ephilida ♂								20	1
P. fusca ♂					2				
P. curialis ♂					1				
P. quercus ♂	1	9	2	17	2	1			

A total of 202 *Phyllophaga* were taken between 5/11/00 and 9/14/00.

Table 19. Georgia, Griffin 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂								1	
P. ephilida ♂								1	
P. forsteri ♂		5		3					
P. ilicis ♂						1			
P. quercus ♂					1				

A total of 12 *Phyllophaga* were taken between 4/22/99 and 7/18/99.

Table 20. Georgia, Tifton 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. glaberrima ♂		4	3						
P. luctuosa ♂	1								
P. mariana ♂		1	2						
P. postrema ♂								3	
P. quercus ♂			1		2				
P. ulkei ♂								1	
P. uniformis ♂		179	135	108	18				

A total of 458 *Phyllophaga* were taken between 4/16/99 and 7/30/99.

Table 21. Georgia, Tifton 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. clypeata ♂			1				1		
P. georgiana ♂	2								
P. glaberrima ♂		15	7	2					
P. lota ♂			1		3	1			
P. mariana ♂			1						
P. quercus ♂					2				
P. uniformis ♂	2	100	205	118	6	1			1
P. uniformis ♀		1		1				1	1

A total of 473 *Phyllophaga* were taken between 5/22/00 and 9/1/00.

Table 22. Iowa, Ames, East Reactor Woods 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂		1							
P. futilis ♂			1		1	1	1	60	

A total of 65 *Phyllophaga* were taken between 5/19/99 and 6/28/99.

Table 23. Iowa, Ames, East Reactor Woods 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂							1		
P. futilis ♂								12	
P. rugosa ♂			1						
P. futilis ♀						1			

A total of 15 *Phyllophaga* were taken between 6/5/00 and 7/10/00.

Table 24. Indiana, West Lafayette 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. balia ♂								2	
P. ephilida ♂								5	
P. fraterna ♂			1						
P. futilis ♂						1	4	55	

A total of 68 *Phyllophaga* were taken between 5/30/00 and 8/17/00.

Table 25. Kansas, Greensburg #1 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. corrosa ♂		13	24	17	4				
P. crassissima ♂				5	7	2	14	2	
P. gracilis angulata ♂								5	
P. lanceolata ♂		1							
P. rubiginosa ♂		1	6	5		1			
P. submucida ♂				3	1	1			

A total of 112 *Phyllophaga* were taken between 4/29/00 and 7/30/00.

Table 26. Kansas, Greensburg #2 2001
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. congrua ♂	211	33							
P. corrosa ♂		1							
P. crassissima ♂	1	6	7	23	189	640	1593	277	7
P. praetermissa ♂	35	583	945	693	100	7	9	7	11
P. rubiginosa ♂	1	18	5	11	2	11			
P. crassissima ♀				1					4
P. rubiginosa ♀				2					1

A total of 5434 *Phyllophaga* were taken between 4/29/01 and 6/20/01.

Table 27. Kansas, Manhattan #1 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. affabilis ♂					7	29	22		
P. bipartita ♂			1		1			13	
P. crassissima ♂		1	4	15	56	96	90		
P. ephilida ♂								28	
P. fusca ♂						2	5		
P. futilis ♂						3	1	50	
P. glabricula ♂	1	41	112	34	10				
P. implicita ♂	1								
P. inversa ♂	155	13	2						
P. rubiginosa ♂	1	30	43	66	18	4			
P. sylvatica ♂		1	1	4	1				

A total of 962 *Phyllophaga* were taken between 5/4/00 and 8/22/00.

Table 28. Kansas, Manhattan #2 2001
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. affabilis ♂						7	10	2	
P. bipartita ♂								23	
P. crassissima ♂				1	15	71	65		
P. ephilida ♂								28	
P. fusca ♂	1	4	1	11	23	63	101	11	
P. futilis ♂						1	3	47	
P. glabricula ♂		8	34	31	2	1			
P. inversa ♂	153	21							
P. rubiginosa ♂	5	143	389	295	405	107	21	1	
P. rugosa ♂		1							
P. sylvatica ♂		18	25	39	13	2			
P. vehemens ♂	29	7	2			1	3		

A total of 2245 *Phyllophaga* were taken between 4/30/01 and 8/16/01.

Table 29. Kentucky, Lexington 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. ephilida ♂	4	2	1	3	1	17	3	455	5
P. fusca ♂		3	5	10	14	8	5		
P. futilis ♂	2		1	3	3	15	72	445	1
P. hirticula ♂			1					3	
P. inversa ♂	15	4	1						
P. rugosa ♂	1	32	64	17	2			2	3
P. ephilida ♀		2				1			1
P. futilis ♀			1			1			
P. rugosa ♀		2							

A total of 1231 *Phyllophaga* were taken between 4/22/99 and 8/20/99.

Table 30. Kentucky, Lexington 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. ephilida ♂	11	5	5	1	2	3	9	994	2
P. fusca ♂		2	5	2	3	11	9		
P. futilis ♂	1	10	5	7	2	247	209	1359	6
P. hirticula ♂		1		2			5	146	4
P. inversa ♂	65	2							
P. rugosa ♂	17	593	504	76	8	3	1	1	2
P. futilis ♀									1
P. rugosa ♀		3	1						

A total of 4347 *Phyllophaga* were taken between 5/2/00 and 8/11/00.

Table 31. Louisiana, Chase 1997
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. ephilida ♂				1	1	
P. forbesi ♂					10	
P. quercus ♂		15	15	9		
P. taxodii ♂				2		

A total of 53 *Phyllophaga* were taken between 6/17/97 and 8/15/97.

Table 32. Massachusetts, South Amherst 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	4	6	2	2			3	291	
P. drakei ♂								1	
P. forsteri ♂		7	12	4	1				
P. fraterna ♂		12	16	5		1			
P. fusca ♂		2	14	68	62	59	7		1
P. gracilis ♂							1		
P. longispina ♂								57	
P. anxia ♀		1					1		

A total of 642 *Phyllophaga* were taken between 5/7/99 and 7/20/99.

Table 33. Massachusetts, South Amherst 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	4	1					1	76	
P. forsteri ♂		1	3		1				
P. fraterna ♂		2	6						
P. fusca ♂		1	1	2	5	5	1		
P. gracilis ♂								1	
P. longispina ♂							1	45	

A total of 157 *Phyllophaga* were taken between 5/8/00 and 7/28/00.

Table 34. Massachusetts, Carver 1996
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. anxia ♂	18	700	591	515	7	3
P. drakei ♂					1	
P. anxia ♀		1		3		

A total of 1839 *Phyllophaga* were taken between 6/4/96 and 6/10/96.

Table 35. Massachusetts, Carver 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. anxia ♂	13	67	627	682	608	54	11	10
P. drakei ♂							1	
P. forsteri ♂		4						
P. anxia ♀		1	1	2			1	

A total of 2082 *Phyllophaga* were taken between 5/22/98 and 7/7/98.

Table 36. Massachusetts, Carver 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	1	115	302	440	514	232	88	2	2
P. crenulata ♂		1							
P. drakei ♂								1	
P. anxia ♀		1	1			1			2

A total of 1703 *Phyllophaga* were taken between 5/20/99 and 7/12/99.

Table 37. Massachusetts, Carver 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	1	127	318	365	356	169	79	2	2
P. drakei ♂								2	
P. forsteri ♂		1							
P. hirsuta ♂								1	
P. anxia ♀			1					1	3

A total of 1428 *Phyllophaga* were taken between 5/15/00 and 7/10/00.

Table 38. Massachusetts, Lakeville 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	77	114	97	38	26	9		2	
P. drakei ♂								1	
P. forsteri ♂		8	4	2					
P. fusca ♂				2	3				
P. gracilis ♂								1	
P. hirsuta ♂								1	
P. marginalis ♂	1								
P. crenulata ♀		1							

A total of 390 *Phyllophaga* were taken between 5/10/99 and 7/12/99.

Table 39. Massachusetts, Lakeville 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	23	22	27	12	2		1		
P. drakei ♂								2	
P. forsteri ♂		15	4	1					
P. fusca ♂						1			
P. marginalis ♂	2								

A total of 112 *Phyllophaga* were taken between 5/2/00 and 7/12/00.

Table 40. Massachusetts, Plympton #1 1996
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. anxia ♂	8	151	128	105		
P. drakei ♂					1	
P. forsteri ♂		3				
P. fraterna ♂			1			
P. anxia ♀						1

A total of 392 *Phyllophaga* were taken between 6/4/96 and 6/10/96.

Table 41. Massachusetts, Plympton #2 1996
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. anxia ♂	12	146	128	110	2	3
P. drakei ♂					2	
P. forsteri ♂			2			
P. fusca ♂		1				

A total of 406 *Phyllophaga* were taken between 6/4/96 and 6/10/96.

Table 42. Maine, Lincolnville Center 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	327	169	92	16	5	2	4	119	
P. drakei ♂								2	
P. fusca ♂		2	2	9	7	2			
P. fraterna ♂	1	8	1	4	1				
P. anxia ♀			1						

A total of 774 *Phyllophaga* were taken between 5/18/99 and 7/2/99.

Table 43. Maine, Lincolnville Center 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	665	272	152	52	6	2	8	128	
P. drakei ♂								1	
P. fusca ♂		1	2	3	4	5			
P. fraterna ♂		1	4	1					
P. marginalis ♂	1								
P. anxia ♀				1					

A total of 1310 *Phyllophaga* were taken between 5/22/00 and 8/21/00.

Table 44. Minnesota, St. Paul #1 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂							2		
P. futilis ♂			1				1	31	
P. rugosa ♂			1						

A total of 36 *Phyllophaga* were taken between 6/7/99 and 6/13/99.

Table 45. Minnesota, St. Paul #1 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂						2		1	
P. futilis ♂				1		4	2	103	
P. rugosa ♂		2	1		1				
P. futilis ♀	1	1				1			
P. rugosa ♀	2	2				1			

A total of 125 *Phyllophaga* were taken between 6/9/00 and 6/30/00.

Table 46. Minnesota, St. Paul #2 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	5								
P. futilis ♂							1	6	
P. nitida ♂		1							
P. rugosa ♂		2							

A total of 15 *Phyllophaga* were taken between 6/9/00 and 6/30/00.

Table 47. Mississippi, Leroy Percy State Park 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. congrua ♂	24	15	7	4				1	1
P. crassissima ♂				1	2				
P. hirtiventris ♂	441	206	69	7	4	1	1	2	2
P. congrua ♀			2				2		1
P. hirtiventris ♀				1					

A total of 794 *Phyllophaga* were taken between 5/5/00 and 6/26/00.

Table 48. Mississippi, Sharkey County, 5 miles SE of Anguilla 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. congrua ♂	213	158	146	48	21	2		1	1
P. hirtiventris ♂	24	10	5	1					
P. perlonga ♂						1			
P. profunda ♂			1						
P. congrua ♀					1			1	

A total of 667 *Phyllophaga* were taken between 5/12/00 and 6/22/00.

Table 49. Mississippi, Stoneville 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂								1	
P. congrua ♂	114	116	69	30	4		8		
P. crassissima ♂			2	21	26	2			
P. ephilida ♂	1							1	
P. hirtiventris ♂	442	324	183	19	10		1		1
P. perlonga ♂							1		
P. congrua ♀		1		1	3	6	1	2	1
P.hirtiventris ♀	1				1			1	1

A total of 1395 *Phyllophaga* were taken between 5/3/00 and 7/10/00.

Table 50. Nebraska, Lincoln 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. crassissima ♂			25	19	44	24	1	
P. crenulata ♂	1							
P. futilis ♂			1	1	1	31	355	
P. inversa ♂		1						
P. vehemens ♂	1							

A total of 569 *Phyllophaga* were taken between 5/15/98 and 6/29/98.

Table 51. Nebraska, Lincoln 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. crassissima ♂			5	23	82	113	87		
P. crenulata ♂	5								
P. fusca ♂						2	3		
P. futilis ♂		1	4	9	11	11	20	924	
P. implicita ♂		2							
P. vehemens ♂	31	1							
P. futilis ♀			1						
P. implicita ♀			1						1

A total of 1337 *Phyllophaga* were taken between 5/16/99 and 7/10/99.

Table 52. Nebraska, Lincoln 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. crassissima ♂			1	16	76	41	38		
P. crenulata ♂		1							
P. fusca ♂						1	2		
P. futilis ♂		2		2	3	6	18	489	
P. rugosa ♂			1						
P. vehemens ♂	3	1							
P. futilis ♀						1			
P. implicita ♀		1							

A total of 703 *Phyllophaga* were taken between 5/10/00 and 7/3/00.

Table 53. New Hampshire, Madbury 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia♂	6	2	2					139	
P. forsteri ♂		1							
P. fraterna ♂		5	2						
P. fusca♂		1	1	3	2	2	1		
P. gracilis ♂							2	12	
P. anxia ♀								1	
P. fraterna ♀		1	1		1				
P. hirticula ♀									1

A total of 186 *Phyllophaga* were taken between 5/9/99 and 8/3/99.

Table 54. New Hampshire, Madbury 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia♂	7	3						30	
P. forsteri ♂			1						
P. fraterna ♂		1	2	2					
P. fusca♂			1	2	1	4			
P. lonispina ♂								2	
P. fusca ♀								1	

A total of 57 *Phyllophaga* were taken between 5/8/00 and 7/17/00.

Table 55. New Jersey, Chatsworth #1 1996
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. anxia ♂					2	
P. forsteri ♂				1		
P. postrema ♂		1			61	

A total of 65 *Phyllophaga* were taken between 5/20/96 and 7/1/96.

Table 56. New Jersey, Chatsworth #1 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. forsteri ♂		1						
P. postrema ♀				1		10	32	

A total of 44 *Phyllophaga* were taken between 5/15/98 and 6/26/98.

Table 57. New Jersey, Chatsworth #1 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. forsteri ♂		1							
P. postrema ♂			1		1	1	1	73	

A total of 77 *Phyllophaga* were taken between 5/24/99 and 7/13/99.

Table 58. New Jersey, Chatsworth #2 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. anxia ♂							1	
P. postrema ♂	1	1		1	1	54	128	
P. postrema ♀						1		

A total of 188 *Phyllophaga* were taken between 5/15/98 and 6/26/98.

Table 59. New Jersey, Chatsworth #2 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. postrema ♂			1			1	2	77	
P. postrema ♀			1			1			

A total of 83 *Phyllophaga* were taken between 6/11/99 and 7/19/99.

Table 60. New Jersey, Chatsworth #2 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂								2	
P. forsteri ♂	1	3	1						
P. postrema ♂		1				6	3	169	
P. postrema ♀					1				

A total of 188 *Phyllophaga* were taken between 5/18/00 and 7/4/00.

Table 61. New Jersey, Hammonton 1996
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	65/35	50/50	35/65	0/100	BLANK
P. anxia ♂					11	
P. forsteri ♂		3				

A total of 14 *Phyllophaga* were taken between 5/11/96 and 7/1/96.

Table 62. New Jersey, New Brunswick 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. crenulata ♂	1								
P. ephilida ♂								2	
P. futilis ♂						2	2	1	

A total of 8 *Phyllophaga* were taken between 6/1/99 and 8/10/99.

Table 63. New York, Bellona 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. anxia ♂	171	76	10	6	2	4	1	
P. fusca ♂			2	5	7			
P. futilis ♂							1	
P. hirticula ♂							1	

A total of 286 *Phyllophaga* were taken between 5/13/98 and 6/26/98.

Table 64. New York, Bellona 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	128	28	4					3	
P. fusca ♂			1	3	4				
P. futilis ♂								3	

A total of 181 *Phyllophaga* were taken between 5/5/99 and 6/18/99.

Table 65. New York, Bellona 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	61	19	6				1		
P. balia ♂								1	
P. futilis ♂							1	2	

A total of 91 *Phyllophaga* were taken between 5/10/00 and 6/12/00.

Table 66. New York, Franklinville 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	282	147	25	2	2	1	3	122	
P. fusca ♂				1	1				
P. futilis ♂								1	
P. marginalis ♂	3								
P. fusca ♀									1

A total of 591 *Phyllophaga* were taken between 5/1/99 and 6/13/99.

Table 67. New York, Riverhead 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. forsteri ♂		1							
P. fusca ♂					1				

A total of 2 *Phyllophaga* were taken between 4/23/99 and 7/16/99.

Table 68. New York, Saratoga Springs 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	5						1	1	
P. fusca ♂		1							

A total of 8 *Phyllophaga* were taken between 5/10/99 and 6/4/99.

Table 69. New York, Saratoga Springs 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	1	1							
P. crenulata ♂							2	1	2
P. crenulata ♀									2

A total of 9 *Phyllophaga* were taken between 5/19/00 and 6/21/00.

Table 70. New York, Warwick 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	48	17	5						
P. balia ♂								1	
P. fusca ♂			13	45	14	20			
P. marginalis ♂	1								

A total of 164 *Phyllophaga* were taken between 5/10/99 and 6/10/99.

Table 71. New York, Warwick 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	66	23	7						
P. balia ♂								1	
P. drakei ♂								21	
P. fusca ♂		1	7	11	25	3			
P. marginalis ♂	2								

A total of 167 *Phyllophaga* were taken between 5/11/00 and 7/20/00.

Table 72. New York, Waterloo #1 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. anxia ♂	299	140	4	3	1	7	33	
P. fusca ♂				1				
P. futilis ♂	1		2	3	2	46	191	
P. futilis ♀				1				

A total of 734 *Phyllophaga* were taken between 5/15/98 and 7/2/98.

Table 73. New York, Waterloo #1 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	695	286	40	5	3	1	16	60	
P. fusca ♂			1	4	7	4	1		
P. futilis ♂	1	1	1	2	2	2	26	165	

A total of 1323 *Phyllophaga* were taken between 5/10/99 and 6/18/99.

Table 74. New York, Waterloo #1 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	404	112	15	1		2	4	17	
P. fusca ♂				2					
P. futilis ♂	1	2		3	9	17	65	309	

A total of 963 *Phyllophaga* were taken between 5/8/00 and 6/19/00.

Table 75. New York, Waterloo #2 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. anxia ♂	84	36	6		1	3	6	
P. futilis ♂	6	1	15	2		65	78	
P. futilis ♀	1	1	1					

A total of 306 *Phyllophaga* were taken between 5/15/98 and 6/26/98.

Table 76. North Carolina, Raleigh #1 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. ephilida ♂				1				61	
P. soror ♂				1					
P. ephilida ♀								1	

A total of 64 *Phyllophaga* were taken between 7/6/99 and 7/26/99.

Table 77. North Carolina, Raleigh #2 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂								2	
P. ephilida ♂	1							33	11
P. forsteri ♂	1	4	2						
P. foxii ♂	1								
P. hirsuta ♂									1
P. micans ♂		5	1	5	19	29	111	1	
P. quercus ♂		5	6	32	5				
P. soror ♂								10	
P. ephilida ♀									1
P. micans ♀				3	2				2
P. soror ♀							1		

A total of 297 *Phyllophaga* were taken between 5/3/00 and 9/5/00.

Table 78. Ohio, Columbus 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂							1		
P. futilis ♂	1	2	2			4	34	212	
P. inversa ♂	7	1				1			
P. kentuckiana ♂	1								
P. futilis ♀	1								

A total of 267 *Phyllophaga* were taken between 5/3/00 and 6/28/00.

Table 79. Ohio, Wooster 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. futilis ♂								1	
P. longispina ♂								1	
P. lota ♂			4	3		6			
P. rugosa ♂		1	2						

A total of 18 *Phyllophaga* were taken between 5/13/00 and 6/20/00.

Table 80. Pennsylvania, State College 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	3	1							
P. fusca ♂		4	4	34	60	71	17		
P. futilis ♂		1					12	333	
P. fraterna ♂	1	2	3	3	3	1			
P. fraterna-like ♂								18	
P. inversa ♂	9								
P. fusca ♀								1	
P. futilis ♀	2			1					
P. fraterna ♀					1				

A total of 585 *Phyllophaga* were taken between 5/7/99 and 7/2/99.

Table 81. Pennsylvania, State College 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	2	1							
P. fusca ♂				4	4	3	1		
P. futilis ♂	1			1	3	4	92	445	1
P. fraterna ♂		2		3					
P. fraterna-like ♂								19	
P. inversa ♂	1								
P. futilis ♀		1							

A total of 588 *Phyllophaga* were taken between 5/1/00 and 6/28/00.

Table 82. Rhode Island, Kingston 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	136	449	512	336	218	106	31	17	14
P. forsteri ♂		1	4	1					
P. fusca ♂				1					
P. anxia ♀	1	2	2	4	4	2	3	3	3

A total of 1850 *Phyllophaga* were taken between 5/14/99 and 6/25/99.

Table 83. Rhode Island, Kingston 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	14	58	59	42	16	1	2	20	1
P. forsteri ♂		1							
P. marginalis ♂	5								
P. anxia ♀					1		3		

A total of 224 *Phyllophaga* were taken between 5/15/00 and 7/5/00.

Table 84. South Carolina, Anderson County 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. ephilida ♂							2	13	
P. fervida ♂								3	
P. hirticula ♂								1	1
P. quercus ♂			1						
P. fervida ♀								1	

A total of 22 *Phyllophaga* were taken between 5/12/99 and 8/20/99.

Table 85. Texas, Dallas #1 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. congrua ♂	531	307	42	16	5		3	3
P. crassissima ♂			81	147	426	137	6	1
P. crinita ♂						1	1	
P. hirtiventris ♂		1						
P. torta ♂						1		
P. crassissima ♀							2	
P. torta ♀		1						

A total of 1712 *Phyllophaga* were taken between 4/22/98 and 6/15/98.

Table 86. Texas, Dallas #1 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. congrua ♂	42	30	58						
P. crassissima ♂					5	14	10		

A total of 159 *Phyllophaga* were taken between 5/13/99 and 5/19/99.

Table 87. Texas, Dallas #1 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. congrua ♂	304	168	99	16	5	2		1	
P. crassissima ♂	2	1	5	61	81	205	76	12	1
P. crinita ♂	3		1				1	2	2
P. torta ♂					1		1		
P. crassissima ♀		1					1		

A total of 1053 *Phyllophaga* were taken between 4/28/00 and 6/27/00.

Table 88. Texas, Dallas #2 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. congrua ♂	760	489	45	22	4			
P. crassissima ♂			10	18	59	22	1	
P. crinita ♂	1			2			1	
P. hirtiventris ♂	1	1						
P. rubiginosa ♂					1	1		
P. congrua ♀		2		1				
P. crinita ♀						1		1

A total of 1443 *Phyllophaga* were taken between 4/22/98 and 6/15/98.

Table 89. Texas, Dallas #3 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. congrua ♂	654	711	28	17		2		4
P. crassissima ♂			6	22	95	28	1	
P. crinita ♂			1					
P. hirtiventris ♂	3	1						
P. rubiginosa ♂			1	1				
P. torta ♂						1		

A total of 1576 *Phyllophaga* were taken between 4/22/98 and 6/15/98.

Table 90. Texas, Dallas #4 1998
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	95/5	65/35	50/50	35/65	5/95	0/100	BLANK
P. congrua ♂	533	694	65	27	10	1		2
P. crassissima ♂			30	86	183	44	2	
P. crinita ♂				1				1
P. rubiginosa ♂				1				
P. congrua ♀								1

A total of 1681 *Phyllophaga* were taken between 4/22/98 and 6/15/98.

Table 91. Utah, Salt Lake City 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. drakei ♂								2	

A total of 2 *Phyllophaga* were taken between 6/2/99 and 7/30/99.

Table 92. Vermont, Burlington 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	12	7	5	1	1		1	30	
P. fraterna ♂		2	2						
P. fusca ♂		2	3	2	7	4	3		

A total of 83 *Phyllophaga* were taken between 5/7/99 and 6/20/99.

Table 93. Vermont, Burlington 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	3	9						1	
P. fraterna ♂		1	1						
P. fusca ♂				4	2	2			

A total of 23 *Phyllophaga* were taken between 5/21/00 and 7/5/00.

Table 94. Wisconsin, Babcock 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	181	30	6	8	7	3	8	12	2
P. rugosa ♂		2	1		1				
P. anxia ♀		1							

A total of 262 *Phyllophaga* were taken between 5/7/99 and 6/29/99.

Table 95. Wisconsin, Babcock 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. anxia ♂	259	63	19	2	4	12	25	20	1
P. drakei ♂								9	3
P. rugosa ♂		1							
P. anxia ♀		1							

A total of 419 *Phyllophaga* were taken between 5/1/00 and 7/10/00.

Table 96. Wisconsin, Verona 1999
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. fusca ♂					1				
P. futilis ♂				2		1	9	265	
P. rugosa ♂		2	4						

A total of 287 *Phyllophaga* were taken between 5/13/99 and 6/28/99.

Table 97. Wisconsin, Verona 2000
Blends indicate the ratio of the methyl esters of L-valine/L-isoleucine

	100/0	90/10	80/20	60/40	40/60	20/80	10/90	0/100	BLANK
P. fusca ♂					1	1			
P. futilis ♂			1		1		6	322	
P. nitida ♂		1							
P. rugosa ♂	2	31	11						
P. futilis ♀					2				

A total of 380 *Phyllophaga* were taken between 5/9/00 and 6/23/00.

Table 98a. Synchronic species captured by the same or nearby sex attractant blends, by state.

State	Location	Year	***Phyllophaga* species**	Blend
AL	Auburn	1997	*gracilis, hirticula*	0/100
AL	Auburn	1998	*anxia, gracilis, hirticula, postrema, ulkei*	0/100
AL	Marion Junction	1999	*davisi, futilis*	0/100
AL	Marion Junction	2000	*gracilis* var. *angulata, forbesi*	0/100
CT	Vernon	1999	*forsteri, fraterna, fusca*	v/i blends
CT	Vernon	2000	*forsteri, fraterna, fusca*	v/i blends
GA	Athens	2000	*aemula, quercus*	v/i blends
GA	Tifton	1999	*glaberrima, uniformis postrema, ulkei*	v/i blends 0/100
GA	Tifton	2000	*glaberrima, uniformis*	v/i blends
IN	West Lafayette	2000	*balia, futilis*	0/100
KS	Greensburg #1	2000	*corrosa, crassissima, rubiginosa*	v/i blends
KS	Greensburg #2	2001	*congrua, crassissima, praetermissa, rubiginosa*	v/i blends
KS	Manhattan #1	2000	*crassissima, fusca, rubiginosa, sylvatica, bipartita, futilis*	v/i blends 0/100
KS	Manhattan #2	2001	See Figure 131	
KY	Lexington	1999	*futilis, hirticula*	0/100
KY	Lexington	2000	See Figure 132	0/100
MA	South Amherst	1999	See Figure 133	
MA	South Amherst	2000	*forsteri, fraterna, fusca anxia, longispina*	v/i blends 0/100
MA	Carver	1998	*anxia, forsteri*	v/i blends
MA	Carver	2000	*anxia, forsteri*	v/i blends
MA	Lakeville	1999	*anxia, forsteri, fusca*	v/i blends
MA	Lakeville	2000	*anxia, forsteri*	v/i blends
MA	Plympton #1	1996	*anxia, forsteri, fraterna*	v/i blends
MA	Plympton #2	1996	*anxia, forsteri, fusca*	v/i blends
ME	Lincolnville Center	1999	*fraterna, fusca*	v/i blends

Table 98b. Synchronic species captured by the same or nearby sex attractant blends, by state.

State	Location	Year	***Phyllophaga* species**	Blend
ME	Lincolnville Center	2000	*fraterna, fusca*	v/i blends
MS	Leroy Percy State Park	2000	*congrua, hirtiventris*	v/i blends
MS	Sharkey County	2000	*congrua, hirtiventris*	v/i blends
MS	Stoneville	2000	*congrua, crassissima, hirtiventris*	v/i blends
NC	Raleigh #2	2000	*forsteri, micans ephilida, soror*	v/i blends 0/100
NE	Lincoln	1999	*crassissima, fusca*	v/i blends
NE	Lincoln	2000	*crassissima, fusca*	v/i blends
NH	Madbury	1999	*forsteri, fraterna, fusca*	v/i blends
NH	Madbury	2000	*forsteri, fraterna, fusca anxia, longispina*	v/i blends 0/100
NJ	Chatsworth #1	1996	*anxia, postrema*	0/100
NJ	Chatsworth #1	1998	*anxia, postrema*	0/100
NJ	Chatsworth #2	2000	*anxia, postrema*	0/100
NY	Bellona	1998	*futilis, hirticula*	0/100
NY	Warwick	2000	*balia, drakei*	0/100
NY	Waterloo #1	1998	*anxia, futilis*	0/100
NY	Waterloo #1	1999	*anxia, futilis*	0/100
NY	Waterloo #1	2000	*anxia, futilis*	0/100
NY	Waterloo #2	1998	*anxia, futilis*	0/100
PA	State College	1999	*fraterna, fusca*	v/i blends
PA	State College	2000	*fraterna, fusca*	v/i blends
RI	Kingston	1999	*anxia, forsteri*	v/i blends
TX	Dallas #1	1998	*congrua, crassissima*	v/i blends
TX	Dallas #2	1998	*congrua, crassissima*	v/i blends
TX	Dallas #3	1998	*congrua, crassissima*	v/i blends
TX	Dallas #4	1998	*congrua, crassissima*	v/i blends
VT	Burlington	1999	*fraterna, fusca*	v/i blends