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Geographic Variation of Sex Ratio in *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae)

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Abstract.—The relative abundance of males and females of *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae) was examined on the basis of specimens held in natural history collections. The species may be divided into two groups of populations. Those in the United States and Canada (between 28°N and 51°N) are primarily thelytokous: males form only 4% of the total number of individual specimens. Populations from localities 23°N and southward have a substantially higher frequency of males (36%). Within each group of populations, there is no demonstrable change in sex ratio with latitude. Male emergence dates generally precede those of females, but there seems to be no significant difference in the time period in which the two sexes are flying. Within the U.S. and Canada, the uncommon males are not randomly distributed.

The parasitoid wasp *Pelecinus polyturator* (Drury) (Hymenoptera: Pelecinidae) is a large and familiar inhabitant of moist deciduous forests in the Nearctic. Its range extends well beyond this, generally from southeastern Canada to central Argentina (Muesebeck 1979, Masner 1993). Surprisingly little is known of *Pelecinus* biology despite its relative abundance. The few published host records indicate that this wasp is an internal larval parasitoid of soil-dwelling Scarabaeidae (Coleoptera) (summarized in Lim *et al.*, 1980). One aspect of its biology that has received wide comment, however, is that males are extremely uncommon in the northern portion of the range.

Brues (1928) cited *Pelecinus polyturator* as an example of the phenomenon of geographic parthenogenesis. Arrhenotokous parthenogenesis is the most common mode of reproduction in the Hymenoptera, in which males are usually produced from unfertilized eggs. Thelytoky is not at all rare, being known from at least twenty families (Stouthamer *et al.* 1990). *Pelecinus* appears to demonstrate both modes: thelytoky in the north temperate region and arrhenotoky elsewhere.

At the time that he wrote his paper Brues admitted that he had seen very few male specimens of *P. polyturator* from the United States or Canada. His analysis of the sex ratio of the species was anecdotal. His sampling of *Pelecinus* was never described and must have been quite limited (see below). Neither did he actually quantify observed sex ratios in tropical and temperate regions. Our purpose here is to quantify the issue of sex ratio variation in this wasp throughout its geographical range.

MATERIALS AND METHODS

Specimen data.—Our information on the distribution and relative abundance of males and females is based upon an extensive survey of the holdings of *Pelecinus* in natural history collections. Material for this study was borrowed or data acquired from 91 collections around the world (see Appendix). The information associated with specimens varies extensively in accuracy and completeness, especially given the small size of the typical label attached to a specimen.

The data were transcribed and stored in a specimen-level relational database. The table structure is slightly modified from the information model developed by the Association of Systematics Collections (1993) and is implemented in the Oracle7® environment on a Silicon Graphics (UNIX) workstation. This combination of hardware and software was chosen to deal with the large numbers of specimens in insect collections and for its ability to interface with other software (geographic information systems, mapping software, and World Wide Web servers). The database stores all of the information on specimen labels (place, time, method of collection, etc.), characteristics of the specimens (e.g., sex, color pattern), source of material, and literature references. The relational structure allows the development of ad hoc queries unconstrained by the format of the original data. As such, the system is not only suited to the questions we ask here, but is also applicable to collection management, diversity assessments, taxonomic studies, host-parasitoid biology, etc. The database (Johnson & Musetti 1996), intended to represent the sum of documented geographic and temporal information available, contains data from 7,188 specimens of the genus *Pelecinus*.

Latitude and longitude of collecting localities were added where these could be determined with relative confidence. These are stored in two separate tables, for points and polygons, reflecting the level of accuracy of the cited collecting locality and our ability to locate the sites in atlases and gazeteers. Only those classed as "points" were used in the analyses below. In practice, this means that the collecting records for points consist of localities identified with specific populated places, recreational areas, manmade features (e.g., monuments), or geographic features such as mountains and lakes.

Brues (1928) pointed out that Neotropical specimens of *Pelecinus* exhibit notable variation in color patterns. Many of these were described as distinct species in the early 19th Century, but the present taxonomic consensus (dating from Schletterer 1890) is that only a single species, *P. polyturator,* is recognized as valid. To avoid confounding data from possible distinct species, we chose to include in our analyses only those specimens conforming to the color pattern of specimens from the U.S. and Canada: the head, mesosoma, and metasoma are uniformly black or very dark brown, and the fore wings are clear or gradually infuscate toward the apex. A summary of the numbers of specimens used is presented in Table 1.

Table 1. Numbers of specimens of males and females of *Pelecinus polyturator* used in analyses of sex ratio.

Latitude of localities	Number of ♂♂ [%]	Number of ♀♀ [%]	Total number
25°N–51°N	119 [4.2]	2723 [95.8]	2842
38°S–25°N	616 [38.4]	990 [61.6]	1606
Total	735 [16.5]	3713 [83.5]	4448

Analyses.—Coordinates of latitude and longitude of collecting localities were extracted from the database by sex. Brues (1928) asserted (as does conventional wisdom) that males and females are not identically distributed. This was tested by comparing the cumulative relative frequency distribution of specimens by 1° of latitude using the Kolmogorov-Smirnov test (Sokal & Rohlf 1995).

If there is variation in sex ratio among sites, especially over the vast area occupied by this species, one reason may be that northern females are substantially longer-lived as adults than males, thus leading to an overabundance of females in collection records. To examine this possibility, we sorted the collecting date records for specimens by sex and combined them into groups for each 10 degrees of latitude (from 50°N to 40°S). Collecting dates were expressed in terms of polar co-

Fig. 1. World distribution of *Pelecinus polyturator.*

ordinates by Julian date (1–365) and mean and standard deviation of the dates were calculated for each sex in every 10° band.

Sex ratio data are expressed as the proportion of males in the total population of specimens. Specimens for every 5° band of latitude were pooled and the relationship between sex ratio and latitude of collection examined using regression. For reasons developed below, these data were partitioned into two groups north and south of 25°N. The two partitions then were separately analyzed for relationship between latitude and sex ratio. Finally, on the basis of this data partition, we examined the hypothesis that males in the U.S. and Canada are randomly distributed. Specimens were pooled from blocks of 5° of latitude and longitude and the observed number of specimens was compared using a χ^2 test with that expected using the observed sex ratio of all specimens north of Mexico.

RESULTS

The documented range of *Pelecinus polyturator* extends from a maximum of 51°N in Quebec and Ontario south to 38°S in Argentina (Fig. 1). The species does not occur in Chile or the West Indies (includ-

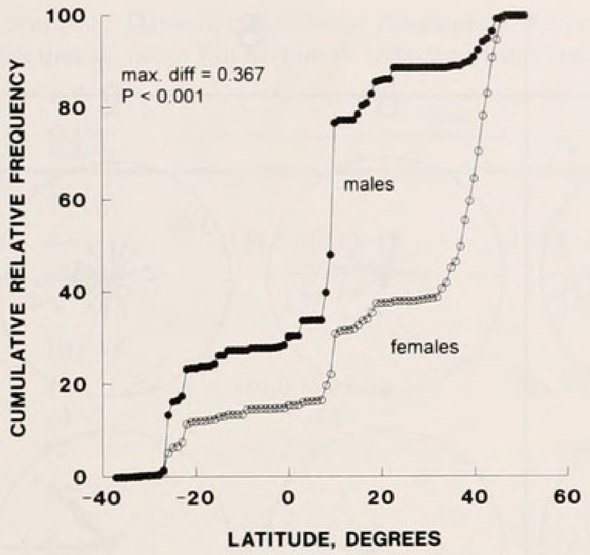

Fig. 2. Cumulative relative frequency distribution (%) of male and female specimens of *Pelicinus polyturator* by latitude. Localities grouped for every 1° of latitude. Maximum difference and probability of identity of distributions using Kolmogorov-Smirnov test.

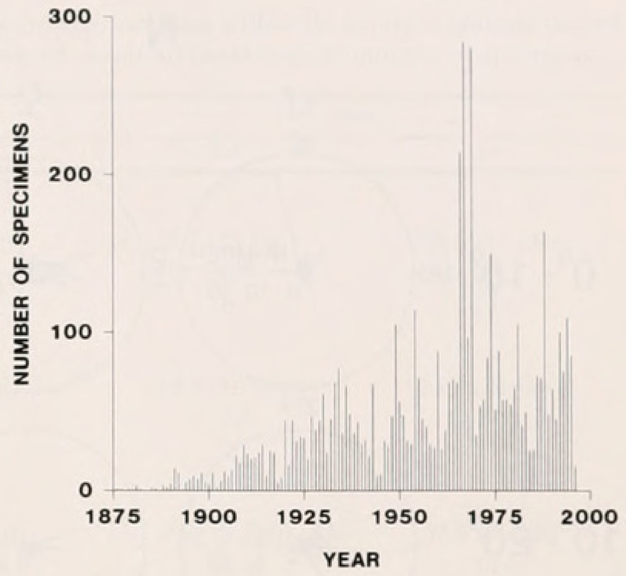

Fig. 3. Frequency distribution of collecting years of *Pelecinus polyturator*. Three specimens collected between 1804 and 1875 are not illustrated.

ing Trinidad). Specimens are otherwise found throughout South America, although material from the Amazon Basin is very scarce. In the United States, the range of the species extends west to 106° in Colorado and New Mexico. The species is apparently absent from peninsular Florida south of the Gainesville area.

The cumulative relative frequency distributions of the two sexes, pooled into 1° increments of latitude, is presented in Fig. 2. The comparison of these two distributions clearly leads to rejection of the null hypothesis that the two are identically distributed throughout America. Specimens of males are clearly more abundant outside of temperate North America.

Two possible sources of sampling error that could lead to the observation of highly skewed sex ratios are (1) the samples were taken in particular years in which one sex is either very rare or extraordinarily abundant, and (2) if populations are strongly protandrous or adult females survive much longer than males, then the apparent rarity of males in some areas may be a collecting artifact. The frequency distribution of collecting dates by year is illustrated in Fig. 3. The distribution of collecting dates for each sex were pooled into groups by 10° of latitude (Fig. 4); statistics for each sex in the latitudinal bands is presented in Table 2. The average collecting dates for males generally precedes those of females, but do not differ significantly. Further, it seems to be possible to find males through most of the flight time of females.

Figure 5 demonstrates a significant negative relationship between latitude and sex ratio (with southern latitude expressed as negative numbers). The observed sex ratio varies from 0.0–0.60, with an average of 0.19. Even cursory examination of the data reveals that this is not a continuous decrease in the frequency of males, but that the change to spanandrous populations (with <10% males) occurs rather abruptly. We have no knowledge of any specimens of *Pelecinus* collected between 23° and 28°N latitude, and the sex ratios on either side of this gap differ strongly. Therefore the data were partitioned into two components at 25°N (Fig. 6). Separate regression analyses result in a change in slope from negative to

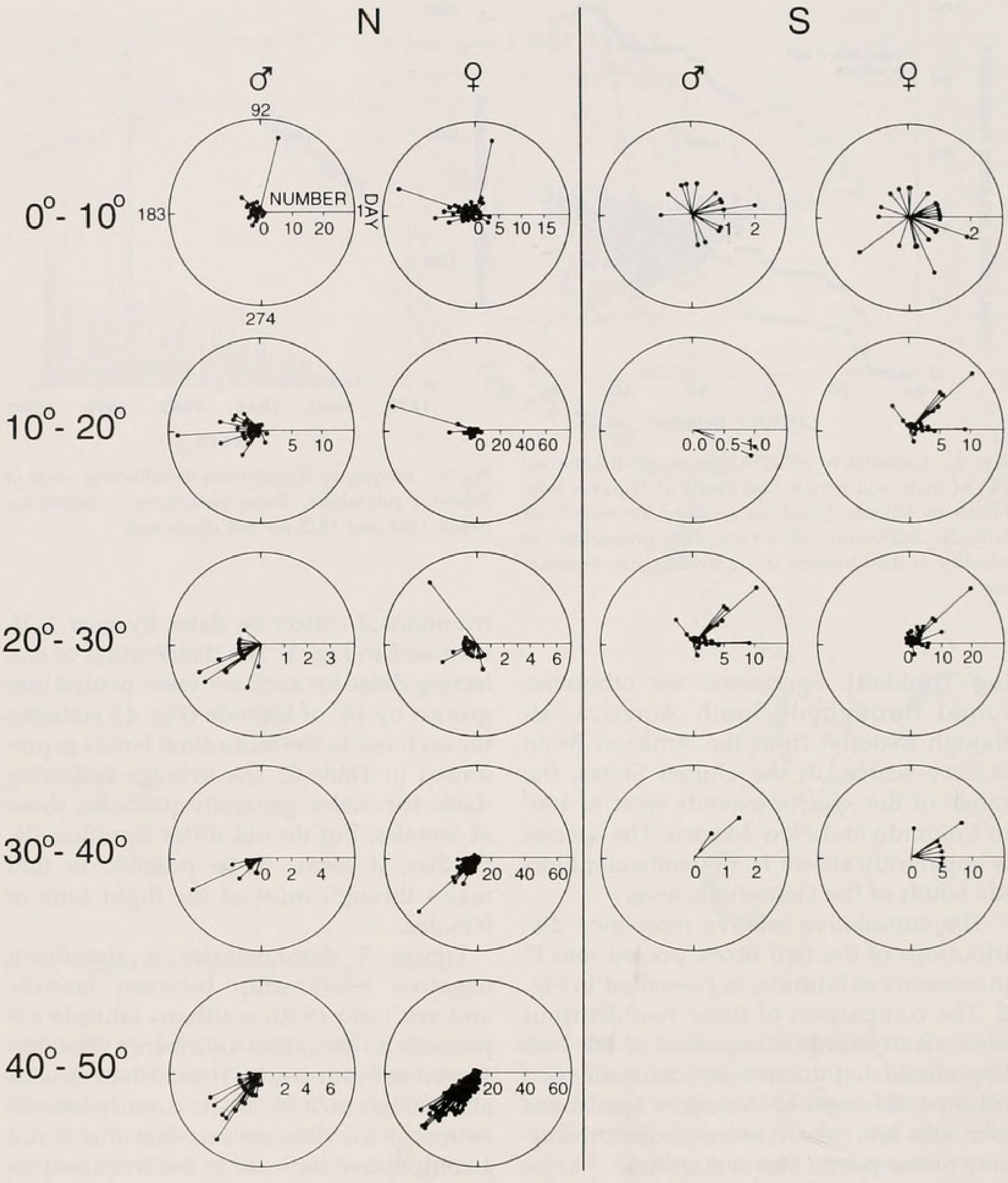

Fig. 4. Collecting dates for males and females of *Pelecinus polyturator*. Localities grouped for every 10° of latitude. Julian day 1 = 1 January; 92 = 2 April; 183 = 2 July; 274 = 1 October; N: north latitudes; S: south latitudes.

positive, but neither significantly differs from a slope of 0, i.e., there is no demonstrable relationship between latitude and sex ratio in the two groups. The average sex ratio for the southern populations is 0.36 (0.20–0.60), and that for the northern populations is 0.04 (0.00–0.06). Figure 7 maps the abundance of males and females in 5° blocks of latitude and longitude. Pooling specimens by latitude or

Table 2. Dates of collection of *Pelecinus polyturator* specimens, localities within 10° bands of latitude pooled together. $\bar{x}$: mean Julian date of collection (calendar date); sd: standard deviation; N: number of specimens.

Degrees latitude	North ♂♂	North ♀♀	South ♂♂	South ♀♀
0°–10°				
$\bar{x}$	144.7 (25 May)	153.4 (2 Jun)	22.7 (23 Jan)	344.8 (11 Dec)
sd	7.1	8.5	20.7	26.3
N	137	222	16	27
10°–20°				
$\bar{x}$	181.0 (30 Jun)	185.7 (5 Jul)	344.0 (10 Dec)	24.3 (24 Jan)
sd	4.8	5.4	0.5	17.9
N	133	390	2	11
20°–30°				
$\bar{x}$	209.3 (28 Jul)	195.9 (15 Jul)	39.0 (8 Feb)	37.5 (7 Feb)
sd	3.4	6.9	12.2	18.5
N	26	30	107	189
30°–40°				
$\bar{x}$	213.2 (1 Aug)	222.4 (10 Aug)	48.3 (17 Feb)	25.7 (26 Jan)
sd	2.3	3.4	0.8	22.0
N	18	897	3	8
40°–50°				
$\bar{x}$	228.1 (16 Aug)	230.7 (19 Aug)		
sd	2.4	2.8		
N	88	1277		

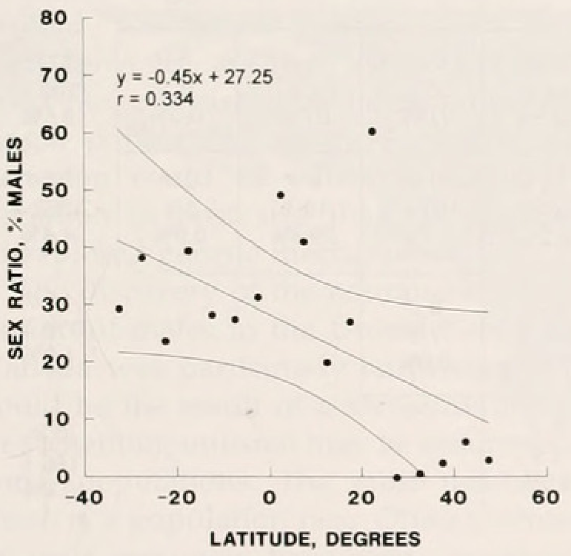

Fig. 5. Sex ratio for all specimens of *Pelecinus polyturator* (proportion of males in total) as a function of latitude, with regression and 95% confidence limits. Individual localities pooled for every 5° of latitude; south latitudes expressed as negative numbers.

longitude (Table 3) reveals that males do not appear to be randomly distributed through the U.S. and Canada.

DISCUSSION

Collecting records are not random samples and we recognize a number of possible biases in the data. Female *Pelecinus* are large and "unusual," easily identifiable, relatively slow fliers, and are often found resting on vegetation at heights accessible to collectors. Thus, females are commonly found in the holdings of even small collections and may be overrepresented. On the other hand, their numerical abundance and the fact that only a single species is recognized may cause experienced collectors to ignore them. Males may be relatively scarce in collections because their abundance in some areas may be truly low, or they may be overrepresented precisely because of their rarity, at least in the eyes of North American col-

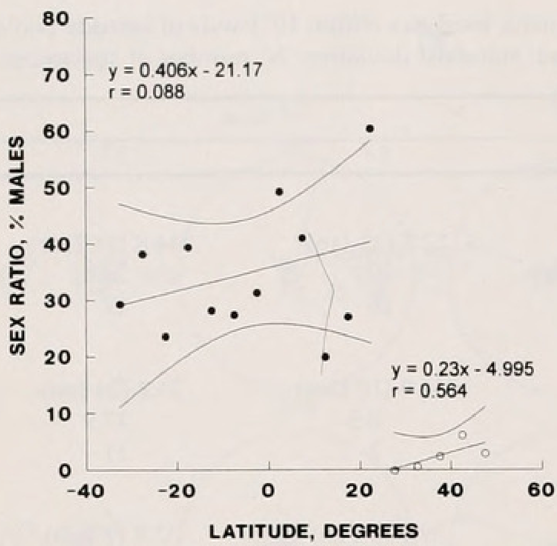

Fig. 6. Sex ratio for *Pelecinus polyturator* (proportion of males in total) as a function of latitude, with regression and 95% confidence limits. Data partitioned into two groups: localities north of 25°N, and localities south of 25°N. Individual localities pooled for every 5° of latitude; south latitudes expressed as negative numbers.

Table 3. Test of null hypothesis that male specimens in Fig. 7 are distributed randomly among blocks in the U.S. and Canada. When pooling by longitude, the specimens from the two westernmost columns of cells and the three easternmost columns of cells were summed to obtain expected numbers greater than five. Expected numbers of males based on overall sex ratio in America north of Mexico: 4.0% males. **: probability < 0.01; *: probability < 0.05.

	χ^2	d.f.
specimens in 5° blocks pooled by latitude	38.6**	2
specimens in 5° blocks pooled by longitude	10.2*	4

lectors. The magnitude and net effect of these biases are impossible to quantify. However these collections represent the material foundation upon which everything we know about this species is based and is the only sample available from which to estimate the sex ratio. We believe that we can fairly judge the hypothesis presented by Brues with cautious use of the specimen data from collections.

Our survey of collections produced only 83 male specimens of *Pelecinus* that we are certain would have been available to Brues (i.e., collected in 1928 or earlier; a further 75 males have no year of collection on the label). Even on the basis of such limited data, it appears that Brues gener-

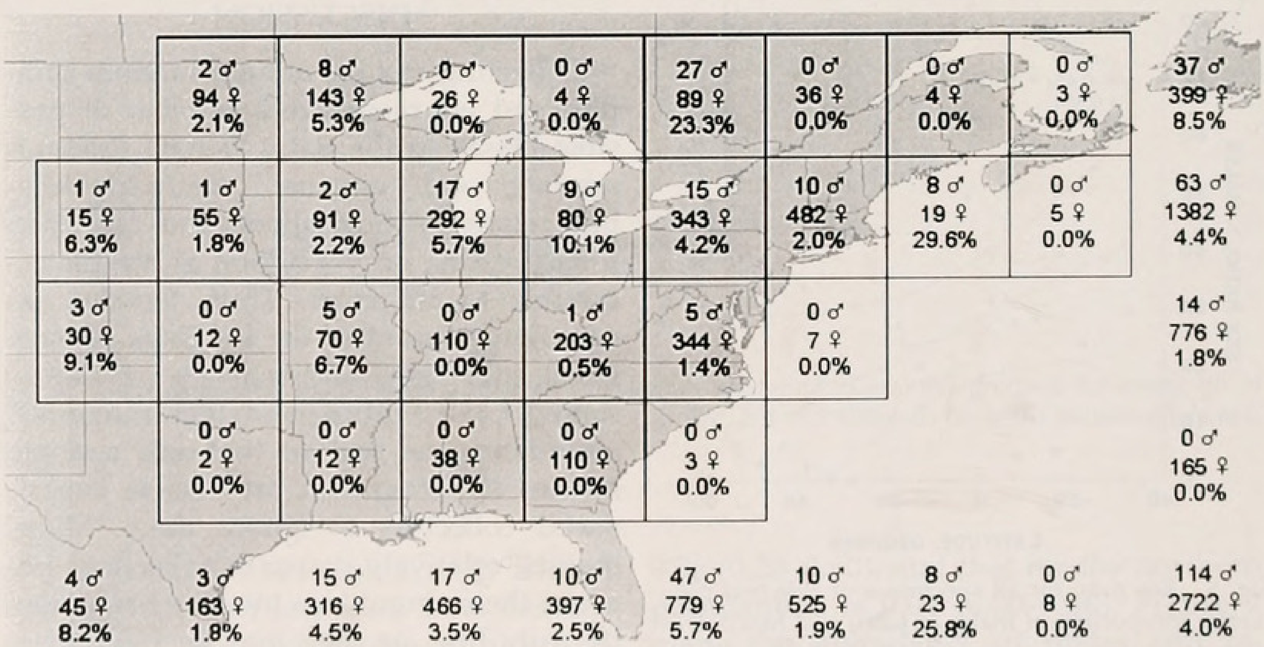

Fig. 7. Numbers of males, females, and sex ratio (proportion of males in total) of thelytokous populations of *Pelecinus polyturator* in blocks of 5° latitude and longitude in the U.S. and Canada.

ally described the true situation: males are very scarce in temperate North America, and elsewhere they occur in numbers consistent with a 0.50 sex ratio. There is an abrupt transition between the two populations that corresponds with a geographical disjunction in southern Texas and northern Mexico. Further focussed collections are needed to determine whether this disjunction is real and, if not, what happens to the males in that area.

We cannot yet identify any diagnostic morphological differences between the northern thelytokous populations and the bisexual populations to the south. Specimens from southern Mexico (Chiapas) and Central America are often distinguishable, but typical black specimens are found from Mexico to Argentina. There is precious little information on the biology of *Pelecinus*, but Aguiar (1997) has recently described the copulatory behavior of individuals in Brazil, consistent with the idea that males in the tropics and south temperate regions are functional, i.e., that females do indeed mate.

Brues (1928) additionally speculated on the genetics of *Pelecinus*. He asserted that the largest specimens were found in the north and suggested that these may be tetraploid. The largest specimens we have seen, however, are from Argentina and a great range of sizes may be found even in single populations in the U.S. The size variation could be better explained by variation in host size than by invoking unexplored genetic mechanisms.

The discovery of the nonrandom distribution of males in the United States and Canada was particularly surprising. This could be the result of a statistical artifact or something unusual may be occurring in some populations. The most notable of these is a population near Ottawa, Ontario: male specimens have been consistently collected in this single site over a period of ten years. Young (1990) described a potentially similar situation in southern Wisconsin in which he suggested that a bisexual population may have replaced the thelytokous strain. The Ottawa population could be a promising one upon which to focus in order to better understand the role of males in the northern temperate populations of *Pelecinus*.

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APPENDIX

Sources of material. American Entomological Institute, Gainesville, FL; American Museum of Natural History, New York, NY; Academy of Natural Sciences, Philadelphia, PA; Buffalo Museum of Science, Buffalo, NY; California Academy of Sciences, San Francisco, CA; Albertson College of Idaho, Caldwell, ID; Carnegie Museum of Natural History, Pittsburgh, PA; Canadian National Collection of Insects, Ottawa, ON; Colorado State University, Fort Collins, CO; Cornell University, Ithaca, NY; Cambridge University Museum of Zoology, Cambridge, UK; Deutsches Entomologisches Institut, Eberswalde, Germany; University of New Hampshire, Durham, NH; College of Environmental Science & Forestry, Syracuse, NY; Denver Museum of Natural History, Denver, CO; Escuela Agrícola Panamericana, Zamorano, Honduras; Estación de Biología "Chamela", UNAM, San Patricio, Mexico; North Carolina Department of Agriculture; University of California, Berkeley, CA; Utah State University, Logan, UT; University of Wyoming, Laramie, WY; Fundação Instituto Oswaldo Cruz, Rio de Janeiro, RJ, Brazil; Field Museum of Natural History, Chicago, IL; Florida State Collection of Arthropods, Gainesville, FL; Instituto Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina; Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica; Illinois Natural History Survey, Urbana, IL; Instituto Nacional de Pesquisas da Amazonia, Manaus, AM, Brazil; University of Wisconsin, Madison, WI; Universidad Central de Venezuela, Maracay, Venezuela; Kansas State University, Manhattan, KS; Natural History Museum, Los Angeles, CA; Loyola University, Chicago, IL; M.A. Ivie private collection; Milwaukee Public Museum, Milwaukee, WI; Museum of Comparative Zoology, Cambridge, MA; Mississippi State University, Mississippi State, MS; Muséum d'Histoire Naturelle, Geneva, Switzerland; Universidad Nacional de La Plata, La Plata, Argentina; Muséum National d'Histoire Naturelle de Paris, France; Michigan State University, East Lansing, MI; Montana State University, Bozeman, MT; Museu de Zoologia da Universidade de São Paulo, São Paulo, SP, Brazil; North Carolina State University, Raleigh, NC; North Dakota State University, Fargo, ND; Naturhistorisches Museum, Vienna, Austria; Naturhistoriska Riksmuseet, Stockholm, Sweden; New York State Museum, Albany, NY; Oklahoma State University, Norman, OK; Ohio State University, Columbus, OH; P.K. Lago private collection; Peabody Museum of Natural History, Yale University, New Haven, CT; Pennsylvania State University, State College, PA; Purdue University, West Lafayette, IN; Museu Nacional, Rio de Janeiro, RJ, Brazil; Pontifícia Universidad Católica del Ecuador, Quito, Ecuador; Nationaal Natuurhistorisch Museum, Leiden, The Netherlands; Royal Ontario Museum, Toronto, Ontario, Canada; R.S. Miller private collection; Rutgers State University, New Brunswick, NJ; R. Willis Flowers collection; South Dakota State University, Brookings, SD; Servicio Entomológico Autónomo, Nicaragua; University of Kansas, Lawrence, KS; Southern Illinois University, Carbondale, IL; Smithsonian Tropical Research Institute, Panama; Texas A&M University, College Station, TX; T.K. Philips private collection; University of Arkansas, Fayetteville, AK; University of Arizona, Tucson, AZ; Universidad de Concepción, Concepción, Chile; University of California, Davis, CA; University of Colorado, Boulder, CO; University of Connecticut, Storrs, CT; University of California, Riverside, CA; University of Delaware, Newark, DE; University of Georgia, Athens, GA; University of Louisville, Louisville, KY; University of Massachusetts, Amherst, MA; University of Mississippi, Oxford, MS; Museum of Zoology, University of Michigan, Ann Arbor, MI; University of Missouri, Columbia, MO; University of Minnesota, St. Paul, MN; Universidad Nacional Autónoma de México, Mexico City, Mexico; University of Nebraska State Museum, Lincoln, NE; National Museum of Natural History, Washington, DC; University of Vermont, Burlington, VT; Virginia Tech University, Blacksburg, VA; University of Idaho, Moscow, ID; James Entomological Collection, Washington State University, Pullman, WA; West Virginia University, Morgantown, WV; Humboldt Universität, Berlin, Germany; Zoologische Staatssammlung, Munich, Germany.