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Insights from specimen data for two economic *Chrysobothris* species (Coleoptera: Buprestidae) in the western United States

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Chrysobothris mali Horn and *Chrysobothris femorata* (Olivier) (Coleoptera: Buprestidae) are wood-boring beetles native to western North America. Both species are highly polyphagous, feeding on a wide range of deciduous trees and shrubs, including fruit and nut trees as well as shade trees grown as nursery stock. *Chrysobothris femorata* is widely distributed across North America, while *C. mali* occurs west of the Rocky Mountains. There is a notable lack of basic biological information regarding both species' phenology and distributions in the Pacific Northwest. To better understand the biology of these economically important insects, seasonal adult collection information, host plant association data, and morphological measurements were collected from preserved specimens residing in 5 major regional arthropod collections. Label information was collected from 661 *C. mali* and 165 *C. femorata* specimens. Collection location data were used to create a map of *C. femorata* and *C. mali* distributions in the western United States, indicating that *C. femorata* is significantly less abundant in California, Oregon, and Washington than *C. mali.* Of the 50 associated plant taxa noted on specimen labels, only 4 associations were shared between the species, potentially indicating host specialization. New reproductive hosts are recorded for *C. femorata* (2 hosts) and *C. mali* (3 hosts). Tree species commonly damaged by flatheaded borers in commercial orchards and nurseries were not present in the historical records. The insights gleaned from specimen data allow researchers to better understand the biology and ecology of these understudied, yet economically impactful insects in the western United States.

Key words: Pacific Northwest, phenology, host, distribution

Introduction

Chrysobothris mali Horn (Pacific flatheaded borer) and *Chrysobothris femorata* (Olivier) (flatheaded appletree borer) (Coleoptera: Buprestidae) are metallic wood-boring beetles native to North America that are known to be economically important pests of tree crops (Seagraves et al. 2013, Wiman et al. 2019, Addesso et al. 2020, Rijal 2020). The range of *C. femorata* extends throughout the United States and Canada, while the distribution of *C. mali* is restricted to west of the Rocky Mountains (Burke and Böving 1929, Fenton 1942, Nelson at al. 2008). Both species are associated with a wide range of woody deciduous host plants including shade, fruit, and nut trees (Lewis 1987, Nelson et al. 2008, Hansen et al. 2012, Seagraves et al. 2013). Adult female *Chrysobothris* spp. lay eggs individually between cracks in the bark of host trees, often targeting points of weakness or injury such as graft unions, pruning scars or sunburned tissue (Burke and Böving 1929, Fenton 1942, Wiman et al. 2019). Larvae chew through the bottom of the egg and immediately tunnel through the outer bark. As the larvae develop, they feed on the cambium and phloem leaving long serpentine galleries that can girdle or severely weaken the tree (Burke and Böving 1929, Fenton 1942). Larval feeding damage leaves trees susceptible to stem breakage during extreme weather events and may completely interrupt the flow of nutrients in the tree, ultimately leading to tree death (Seagraves et al. 2013, Dawadi et al. 2019, Addesso et al. 2020).

There has been an increase of *C. femorata* and *C. mali* damage to commercial tree crops throughout the western United States in recent years (Acheampong et al. 2016, Dawadi et al. 2019, Wiman et al. 2019, Addesso et al. 2020). In western Oregon, increasing impacts from *C. femorata* and *C. mali* damage may be related to rapidly expanding acreage of young commercial hazelnut orchards (Pacific Agricultural Survey 2019, Wiman et al. 2019). New orchards are increasingly planted in suboptimal conditions or in dry-land production systems, leaving transplanted trees vulnerable to attack. *Chrysobothris femorata* and *C. mali* often target trees that are drought or transplant stressed, suggesting that the economic impacts of flatheaded borer attacks may increase as climate change induced droughts become more prevalent on the Pacific Coast (Burke and Böving 1929, Fenton 1942, Xu et al. 2019).

Despite the detrimental economic and projected impacts of these flatheaded borer species in orchard and nursery systems in the western United States, *C. mali* and *C. femorata* are critically understudied. The only information available on the basic biology and damage symptoms of *C. mali* is covered in a handful of publications, and many of the studies were published in the early 20th century. Burke (1917, 1919) published the first notes on the life histories and host plant uses of *C. mali* and *C. femorata* in the western United States. Ten years later, the only comprehensive study detailing the life history of *C. mali* in northern California was published (Burke and Böving 1929). This latter publication included an extensive host plant list, descriptions of development and phenology of the beetle, technical descriptions of all life stages, and descriptions of the extent of *C. mali* damage to managed orchard and landscape trees (Burke and Böving 1929).

The body of *C. femorata* literature is larger due to its wider distribution, recent taxonomic revisions, and its impacts on agriculture in eastern North America (Wellso and Manley 2007, Seagraves et al. 2013, Dawadi et al. 2019, Addesso et al. 2020). Fenton (1937) and Maxwell (1935) thoroughly studied the life history and control of *C. femorata* in Oklahoma and provided a strong foundation of basic biological information. However, life-history information from Fenton (1937) and Maxwell (1935) must now be considered in the context of more recent research establishing that *C. femorata* co-occurs with a suite of cryptic species in its eastern range. Wellso and Manley (2007) revised *C. femorata* into a complex of 12 closely related species, providing some taxonomic clarity to this group of cryptic species. In recent years, *C. femorata* has become a pest of interest in nursery production in the eastern United States, which has led to renewed interest in investigating chemical and cultural control methods (Oliver et al. 2003, 2010, Seagraves et al. 2013, Dawadi et al. 2019, Addesso et al. 2020). Both *C. femorata* and *C. mali* are considered as potential invasive pest species in Europe with high likelihood of entry to the continent through imported nursery stock, sawn wood, and wood packing material from North America (Korycinska et al. 2021).

Although *C. femorata* and *C. mali* have become concerning pests in the Pacific Northwest, no recent literature exists detailing their life histories in this region. The gap in the literature is likely due to inconsistent damage patterns, (Burke and Böving 1929, Fenton 1942, Davis et al. 1968, McNelly et al. 1969) and the protected and cryptic nature of their larval stage. Additionally, reliable monitoring methods are currently unavailable and ambiguous larval feeding signs make mass sampling of adult beetles extremely difficult. To overcome these obstacles, it is critical to collect and compile all available information about flatheaded borer biology to build a strategy for conducting future research on these species in the western United States.

Natural history museums are often underutilized sources of knowledge that can provide useful basic biology information (Graham et al. 2004, Chapman 2005, Baird 2010). Through the compilation of specimen label data and collector notes, researchers can reconstruct the geographic range, phenology, and ecological associations of their subject without ever stepping into the field (Graham et al. 2004). Historic specimens also provide an opportunity to collect data over a wide geographic range and long timeframe. Museum data-mining is particularly useful when studying rare, understudied, or elusive taxa (Graham et al. 2004).

In this research, *C. mali* and *C. femorata* biology in the western United States was explored by examining historic specimens in five major arthropod collections: the Oregon State Arthropod Collection (OSAC), the M.T. James Museum (MTJM), the William F. Barr Museum (WFBM), the Oregon Department of Agriculture collection (ODA), and the California Academy of Sciences collection (CASC). Label information was collected and compiled including collection dates, collection locations, notes on plant associations, and morphological measurements. Using data gleaned from museum specimens, our goal was to gather and summarize basic data for these important species to improve understanding of their distribution, phenology, morphology, and host plant associations in the western United States to aid in future work with these species.

Methods

Label data and morphological measurements were obtained from all preserved adult *C. mali* and *C. femorata* specimens housed in OSAC, MTJM, WFBM, and ODA. To supplement these data, a database of digitized *C. femorata* and *C. mali* specimens from CASC was downloaded from the Global Biodiversity Information Facility (GBIF 2021; gbif.org). Specimen data from CASC were entirely digital, so no morphological measurements were taken. All specimen data were combined into one database.

Most specimens were labeled with location, date collected, and collector information, and some were paired with host or associated plant information. When recording plant associations, the collector often included a note on the association type. Association types included "on," "flying to," "near," "trapped on," and "beating." The term "beating" was assumed to refer to the use of a beat sheet, a common insect collection method. When collectors used the term "cut from" it was assumed that an adult beetle was cut from the plant material shortly before emergence, or that the adult beetle emerged from the excised host plant material after it was cut from the living plant. Adult specimens labeled with "reared" and "cut from" were considered to indicate definite larval hosts, indicating larvae completed their development inside these plant species. Other collections methods were considered possible or likely host associations, depending on the frequency of occurrence. All information contained on the labels was included in the database.

The adult beetle specimens often were housed in labeled unit trays with individuals of the same species. Many had identifier tags attached to the specimen and the identifier was usually an established buprestid expert. Specimens housed in the CASC were utilized in the Wellso and Manley (2007) revision of the *C. femorata* species complex and were identified by Wellso. A small collection of *C. femorata* complex specimens that were identified by Wellso during the 2007 revision were housed in the ODA collection. To avoid including misidentified *C. femorata* complex specimens, the specimens from MTJM, WFBM, and ODA were compared with *C. femorata* and *C. wintu* paratypes using features described in Wellso and Manley (2007).

Along with label information, simple morphological measurements (head width, elytral length, and overall body length taken in millimeters at their widest points) were recorded using a pair of digital calipers (3 in. Carbon Fiber Digital Caliper No. 1433, General Tools & Instruments Co LLC., Secaucus, NJ, USA). Specimens also were sexed, when possible, by examining the posterior edge of the last abdominal sternite (Burke and Böving 1929). Morphological differences between *C. femorata* and *C. mali* and between sexes within the 2 species were compared using a 2-sample *t*-test (α = 0.05). Statistics were analyzed in RStudio (RStudio Team 2021). Apart from the distributional maps, graphics were created using RStudio (RStudio Team 2021), and tables were created using Excel.

Specimen collection location data available from the 5 collections were used to create distribution maps with a focus on the Pacific Northwest and the western United States. Latitude and longitude coordinates were obtained by searching for collection locations from specimen labels in Google Earth Pro (Version 7.3.4.8248). Most specimens were labeled with a state, county, and city. Some contained more precise street addresses or mileage markers. Care was taken to estimate the exact collection location from these directions. A few labels contained county names, and in those instances, the default coordinates assigned to the county were used in place of a specific collection location. In some cases, the collection location was an invalid place name; and consequently, the location was undetermined, and the data points were omitted from mapping efforts. All data points used in the database were combined with publicly available cartographic shape files in the open-source GIS software, QGIS, to create distribution maps (QGIS.org, 2021).

Date of collection data were recorded from the specimen labels. Labels missing month, day, or year information were omitted. The scope for the *C. femorata* phenology assessment was restricted to Pacific Coast states of California, Oregon, and Washington to reduce the number of possible misidentifications of the *C. femorata* complex. All *C. mali* specimens with collection dates were included in the phenology assessment.

Results

Label information was collected from 661 *C. mali* specimens and from 165 *C. femorata* specimens, with sex ratios of (3:2 m:f) and (1:1 m:f), respectively. Specimens in the 5 museum collections were field collected between 1905 and 2009 with a median collection year of 1961. There was a notable gap in collection effort after 1971 (i.e., only 6% [n = 110] of the 664 databased specimens with date labels). The CASC collection database contributed 58 *C. femorata* and 271 *C. mali* specimens with a median collection year of 1971 for *C. femorata* collections, and 1940 for *C. mali* collections. The CASC specimens were not measured and sexed in this study as only digital records were obtained. The OSAC contributed 35 *C. femorata* and 50 *C. mali* with median specimen collection years 1923 and 1958, respectively. The MTJM contributed 18 *C. femorata* specimens and 7 *C. mali* specimens with median collection years of 1936 and 1958, respectively. The WFBM contributed 33 *C. femorata* with a median collection year of 1965, and 191 *C. mali* specimens with a median collection year of 1967. The ODA collection contributed 8 *C. femorata* with a median collection year of 2004, and 155 *C. mali* specimens with a median collection year of 1969. The median collection years at the WFBM and the ODA collection were more recent due to the collection efforts of William F. Barr, Frank M. Beer, and Rick Westcott, who collected 30, 123, and 105 specimens, respectively (Fig. 1; Table 1).

Mean morphological measurements were taken from 106 *C. femorata* collected in California, Oregon, and Washington and 388 *C. mali* specimens collected across its range. The comparisons between species and between sexes within each species were significantly different in all categories (α = 0.05; Fig. 2; Table 2). Adult male and female *C. femorata* differed in average pronotum width (t = 4.76; df = 104; $P < 0.001$), elytral length (t = 3.49; df = 104; $P < 0.001$), and overall body length (t = 5.15; df = 104; $P < 0.001$) when measured at their widest points. Adult male *C. femorata* were smaller than females on average. Adult male and female *C. mali* differed in average pronotum width (t = 4.24; df = 386; $P < 0.001$), elytral length (t = 3.13; df = 386; $P < 0.001$), and overall body length (t = 3.14; df = 386; $P < 0.001$; Table 2). The average *C. mali* male was smaller than an average female of the same species. When comparing the 2 species, *C. mali* was significantly smaller than *C. femorata* in pronotum width (t = 24.58; df = 492; $P < 0.001$), elytral length (t = 27.19; df = 492; $P < 0.001$), and overall body length (t = 27.13; df = 492; $P < 0.001$; Table 2).

Specimen collection dates were recorded from the labels of 127 *C. femorata* representing Pacific Coast states, and 537 *C. mali* specimens collected throughout the western United States to determine the phenology of adults (Fig. 3). The median collection date for *C. femorata* was 10 June, while the median collection date for *C. mali* was 20 June. Both species were collected most frequently in May, June, and July, with peaks in June (Fig. 3). The 22 *C. femorata* individuals collected in March were from California and Oregon, with 9 collected from the Central Valley region, 9 collected from an unverifiable location in California, and 3 collected in Salem, Oregon. *Chrysobothris femorata* was collected from March to September, while *C. mali* was collected from March to August. *Chrysobothris femorata* was present consistently from March to August, and one specimen was collected in San Jose, California in September. Most *C. mali* collections occurred in May, June, and July (i.e., 76.9% [n = 508] of the 661 databased specimens with date labels) with few specimens collected in March, April, and August (Fig. 3). The *C. mali* specimens collected in March were also from the Central Valley of California (7 specimens), however, one specimen was collected from Roseburg, Oregon. One *C. mali* collection was recorded as 31 January in Napa, California; an outlier in the specimen collection dates for both species.

Collection location information was available for 151 *C. femorata* and 608 *C. mali* specimens. The location data were used to create a comprehensive map of *C. femorata* and *C. mali* distributions in the western United States (Fig. 4). California had the highest collection rate of 424 *C. mali* and 94 *C. femorata* specimens.

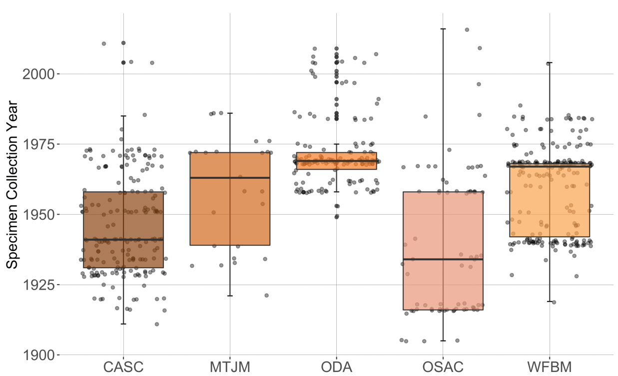

Fig. 1. The distribution of specimen collection years for each natural history museum. California Academy of Science (CASC); M. T. James Museum (MTJM); Oregon Department of Agriculture (ODA); Oregon State Arthropod Collection (OSAC); William F. Barr Museum (WFBM).

Table 1. Specimen counts and collection year ranges of *Chrysobothris femorata* and *Chrysobothris mali* specimens housed in 5 major entomology collections in the western United States

	California Academy of Science		Oregon State Arthropod Collection		William F. Barr Museum		M. T. James Museum		Oregon Dept. of Agriculture	
Species	No. specimens	Date range (median)	No. specimens	Date range (median)	No. specimens	Date range (median)	No. specimens	Date range (median)	No. specimens	Date range (median)
Chrysobothris femorata	59	1931–1973 (1971)	84	1905–2009 (1923)	148	1917–1995 (1965)	65	1911–1976 (1936)	8	1972–2004 (2004)
Chrysobothris mali	271	1911–2004 (1940)	50	1905–1973 (1958)	191	1919–2004 (1967)	7	1921–1986 (1958)	155	1949–2009 (1969)

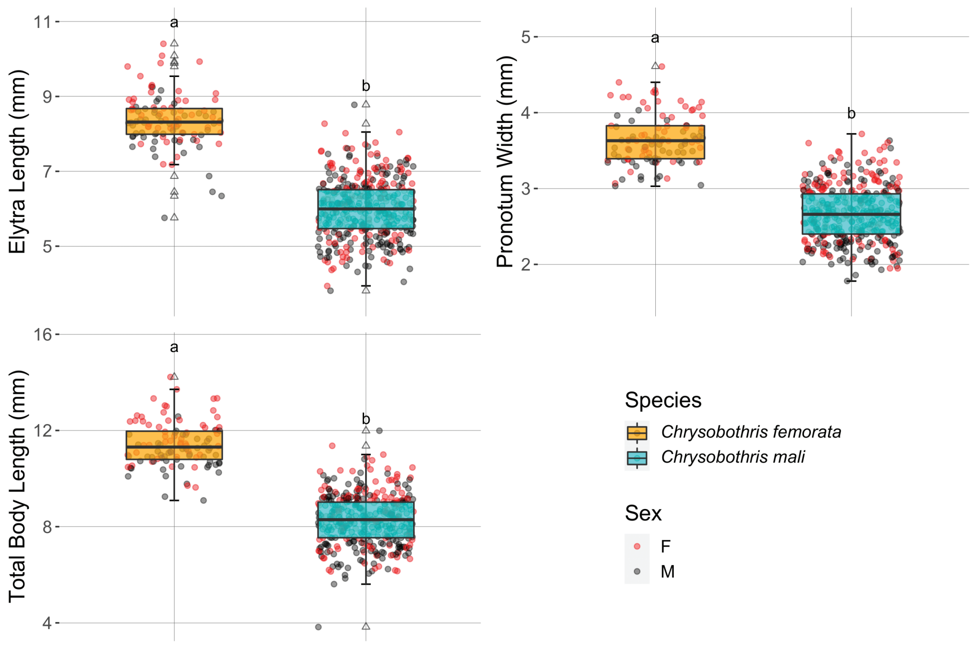

Fig. 2. Boxplots displaying the size distributions for Pacific Coast collected *Chrysobothris femorata* and *Chrysobothris mali* collected throughout California, Oregon, and Washington. Measurements include elytra length, pronotum width, and total body length (mm) recorded at their widest points. Red points represent females, gray points are males, and triangle points are outliers. Letters indicate significant differences.

Table 2. Specimen measurement ranges and means for *Chrysobothris femorata* and *Chrysobothris mali*

Species	Sex	No. specimens	Pronotum width (mm)	Elytra length (mm)	Total body length (mm)
Chrysobothris femorata	♀	52	3.07–4.6 (3.78)	7.18–10.41 (8.57)	9.62–14.22 (11.82)
	♂	54	3.03–4.03 (3.51)	5.76–9.25 (8.11)	9.09–12.58 (10.99)
Chrysobothris mali	♀	150	1.95–3.61 (2.77)	3.94–8.27 (6.16)	6.14–11.36 (8.45)
	♂	238	1.78–3.63 (2.61)	3.81–8.78 (5.89)	5.61–11.99 (8.14)

Pronotum width, elytra length, and total body length were measured at their widest points. All comparisons of measurements made between species were significant under a 2-sample *t*-test ($P < 0.001$). All comparisons between males and females within each species were also significant and are not graphically depicted ($P < 0.001$).

Chrysobothris spp. were collected throughout the state, but collections were highly concentrated in the Central Valley and in southern California. In Oregon, 43 *C. femorata* and 162 *C. mali* were collected with the most sampling occurring east of the Coast Range and west of the Cascade Mountains. Only 5 *C. mali* individuals were collected in Washington state, whereas 27 *C. femorata* were collected throughout the state. The *C. mali* range extended eastward to the Rocky Mountains, confirming that this species is only found in western North America (Fig. 4).

Plant associations were recorded from label data from 64 *C. femorata* and 207 *C. mali* specimens. Both species were associated with a total of 50 plant taxa, however larval (reproductive) host plant data were recorded for only 12 plant species where the collector indicated the adult beetle was 'reared from' or 'cut from' these hosts. After aggregating all previously published hosts (Supplementary Tables S1 and S2), the associated plant information from specimen labels revealed new reproductive hosts for both species (Tables 3 and 4). *Chrysobothris femorata* individuals (19 specimens) were reared

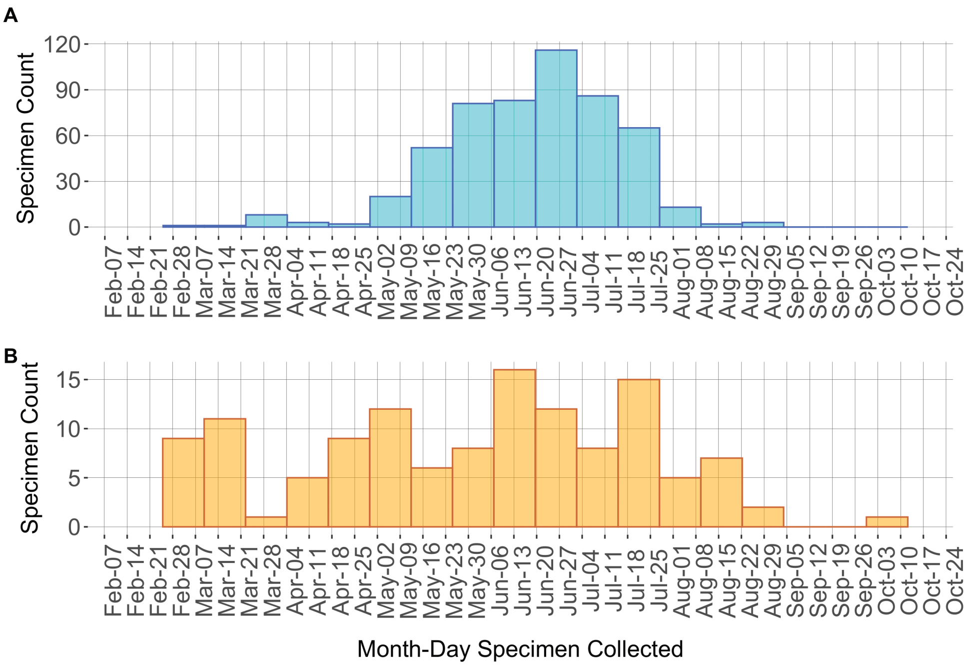

Fig. 3. Phenology curves obtained using collection dates associated with *Chrysobothris femorata* (B) museum specimens collected in California, Oregon, and Washington and *Chrysobothris mali* (A) specimens collected throughout its range.

from *Alnus rubra* Nutt. (1; new host), *Betula occidentalis* Hook (1; new host), *Malus domestica* Borkh. (2), and *Populus fremontii* Wats. (5). *Chrysobothris mali* individuals (26 specimens) were reared from *Amelanchier arborea* (Michx.) Fernald (6; new host), *Ceanothus cuneatus* (Hook.) Nutt. (2), *Cercocarpus ledifolius* Nutt. (1; new host), *Platanus racemosa* Nutt. (3), *Quercus* sp. (1), and *Ribes erythrocarpum* Coville & Leiberg (12; new host).

Other plant taxa are regarded as associations, as the collector indicated that specimens were collected 'on', 'flying to', 'near', or obtained via 'beating'. *Chrysobothris femorata* was associated with 9 plant families, 11 genera, and 17 species (Table 3). *Chrysobothris mali* was associated with 12 plant families, 19 genera, and 36 species (Table 4). The plant associations of *C. mali* and *C. femorata* did not overlap often. Out of the 50 associated plant taxa, only 4 plant species associations were shared between the species (Fig. 6). Both species were associated with *S. lasiandra* Benth., *M. domestica, P. avium* L., and *Platanus racemosa* Nutt. When examining plant families, *C. femorata* and *C. mali* were also divided. *Chrysobothris mali* was strongly associated with the families Rhamnaceae and Rosaceae while *C. femorata* was strongly associated with Salicaceae and Betulaceae (Fig. 5).

Discussion

Understanding the basic biology of economically important pests is vital in guiding establishment of effective management strategies, yet documentation from available literature about the biology of *C. mali* and *C. femorata* is temporally and geographically limited. Work with these taxa is often challenged by the cryptic nature of the flatheaded borer larval stage. In cases where literature is limited, and the subjects are elusive, historical specimen data can be particularly valuable. After compiling information from previously uncatalogued label data associated with 826 flatheaded borer specimens maintained within 5 major western arthropod collections, data were used to determine distributions, phenology, morphological differences, and plant associations.

Location information from specimen labels was used to create the only comprehensive distribution maps for both species in the western United States (Fig. 4). These findings uphold the validity of Burke and Böving's (1929) description of the distributed range of *C. mali*. No *C. mali* specimens were collected in British Columbia, although noneconomically impactful levels of *C. mali* damage have been documented in apple (*M. domestica*) orchards in this region (Acheampong et al. 2016). The map of the distribution of *C. femorata* indicates that *C. femorata* is present in all west coast states, although it may be less abundant than *C. mali*.

The maps of western states illustrate a trend of high concentrations of flatheaded borer collections occurring around large agricultural hubs within each state (Fig. 4). The map of California shows many *C. mali* collections around the Sacramento and San Juaquin valleys. These regions of California are known for high-value tree crop industries such as almonds (*P. dulcis* Mill.) and walnuts (*Juglans* spp.). In Oregon, specimen collections were clustered around the Rogue Valley in the south and the Willamette Valley in the north. Both regions have historically had tree crop industries including orchard crops, blueberries (*Vaccinium* spp.), and ornamentals. Washington is yet another western state with large pear (*Pyrus communis*), apple, and cherry (*Prunus* spp.) industries. Few specimens were collected in Washington in comparison to Oregon and California. However, most of the collections occurred in the Columbia River basin, where high value tree crops are grown (Fig. 4). The historical presence of flatheaded borers in these regions may be cause for concern, as climate change induced droughts intensify in the western United States, providing optimal conditions for flatheaded borer attacks on stressed trees (Burke and Böving 1929, Fenton 1942, Cook et al. 2018).

Chrysobothris mali is more abundant than *C. femorata* where their ranges overlap, as evidenced by the high concentrations of *C. mali* collections in California and Oregon when compared to collection rates of *C. femorata* (Fig. 4). The overlapping distributions of the two species is supported by previous work in the region. Burke and Böving (1929) observed that *C. mali* was the principal damage

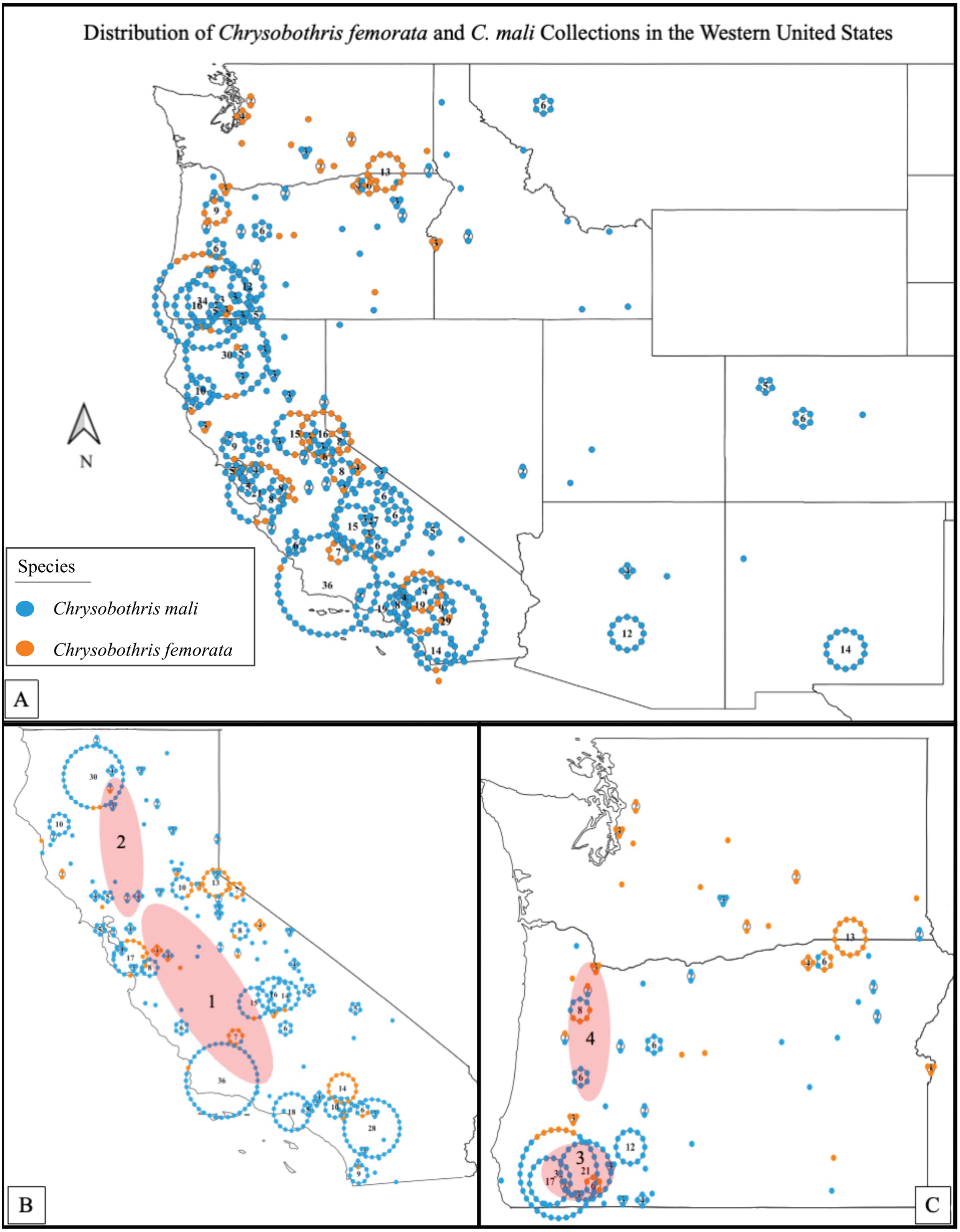

Fig. 4. Maps of *Chrysobothris femorata* and *Chrysobothris mali* distributions in the western United States (A), California (B), and Oregon and Washington (C). The eastern range of *Chrysobothris femorata* is incomplete, as specimens from western entomology collections were utilized in this analysis. Dot rings indicate the number of specimens collected at a single location indicated by the center point, which is also labeled with the specimen count. Red numbered ovals represent the San Joaquin Valley (1), Sacramento Valley (2), Rogue Valley (3), and the Willamette Valley (4).

Table 3. A list of all plant associations on *Chrysobothris femorata* museum specimen labels.

Family	Common name	Plant species	No. observations	Association type
Betulaceae	**Red alder**	***Alnus rubra* Nutt.**	**1**	**Reared (1)**
Betulaceae	White alder	*Alnus rhombifolia* Nutt.	1	On (1)
Betulaceae	**Water birch**	***Betula occidentalis* Hook**	**2**	**Reared (2)**
Betulaceae	Birch	*Betula* sp.	8	Reared (8)
Betulaceae	Japanese hornbeam	*Carpinus japonica* Blume	4	Reared (4)
Myrtaceae	Eucalyptus	*Eucalyptus* sp.	1	ns (1)
Cupressaceae	California incense-cedar	*Calocedrus decurrens* Florin	1	ns (1)
Rosaceae	Apple	*Malus domestica* Borkh.	2	ns (2)
Platanaceae	Western sycamore	*Platanus racemosa* Nutt.	1	Cut from (1)
Salicaceae	Fremont cottonwood	*Populus fremontii* Watson	8	Flying to (2); on (1); reared (5)
Salicaceae	Black poplar	*Populus nigra 'italica'* Du Roi	1	ns (1)
Salicaceae	Quaking aspen	*Populus tremuloides* Michx.	10	ns (10)
Salicaceae	Black cottonwood	*Populus trichocarpa* Torr. & Gray	3	Flying to (1); on (3)
Rosaceae	Sweet cherry	*Prunus avium* L.	3	Trapped in (3)
Rosaceae	Stone fruit	*Prunus* sp.	2	ns (2)
Fagaceae	Oregon white oak	*Quercus garryana* Doug. ex. Hook	2	On (1); flying to (1)
Fagaceae	Chisos red oak	*Quercus gravesii* Sudw.	1	Flying to (1)
Fagaceae	California black oak	*Quercus kelloggii* Newb.	1	ns (1)
Fagaceae	Valley oak	*Quercus lobata* Née	5	ns (5)
Salicaceae	Pacific willow	*Salix lasiandra* Benth.	5	Beating (5)
Salicaceae	Willow	*Salix* sp.	2	On (2)

Bold rows indicate new species records for *Chrysobothris femorata*.

The collection activity was often noted by the collector. "Beating" indicates collection via beat sheet. Adult specimens labeled with "reared" or "cut from" were considered to indicate reproductive host associations. The label "ns" indicates the collector did not specify the association type.

causing agent in western forest and agricultural landscapes. Recent damage to Oregon hazelnuts (*Corylus avellana* L.) and California walnuts has supported this observation (Wiman et al. 2019, Rijal 2020). It is unknown why *C. femorata* may be less abundant in the western relative to the eastern United States. *Chrysobothris femorata* co-exists with a complex of *Chrysobothris* spp. in its eastern range (Wellso and Manley 2007), but it is the principal damage causing agent in the eastern United States (Potter et al. 1988, Oliver et al. 2003, 2010, Seagraves et al. 2013, Dawadi et al. 2019, Addesso et al. 2020).

The maps developed using museum specimen data are informative and novel for *C. mali* and *C. femorata,* but the results may be biased by the collection effort in each region. The Central Valley in California was already a major agricultural region at the turn of the century (Olmstead and Rhode 2017). Burke (1929) may have targeted these areas as priority regions for research as they contained tree crop industries that could be threatened by flatheaded borers. If the Central Valley was sampled more because of its agricultural importance, then it is reasonable to expect higher densities of beetle collections occurring in this region. Additionally, lower numbers of specimens suggest robust sampling efforts have not occurred in northeastern Oregon and the state of Washington although Burke, a pioneer of western entomology, did some work in the Pacific Northwest (Wickman 2005). Increased sampling effort in the Pacific Northwest, particularly in Washington state, would improve the accuracy of range maps developed using this museum specimen database.

The phenology of *C. mali* and *C. femorata* from the Pacific Coast states was determined using the collection dates recorded on specimen labels. A surprisingly high number of *C. femorata* collections occurred in March, where a gradual emergence trend was expected. The small peak of collections in March is likely due to the geographic distributions of the collections. Half of the March collections occurred in the region of the Central Valley of California, where the climate is warmer, and the growing season is longer than in the Pacific Northwest. The other California March collections were from unverified locations in California, but it is probable that those locations were also in central or southern California. The 2 specimens collected in March in Oregon represent outliers. Likely, the small peak in March is due to a lack of *C. femorata* collections on the Pacific Coast, and it is likely that *C. femorata* is present consistently from March to August in California. Further sampling of *C. femorata* is required to obtain a more robust phenology distribution for this species in California, Oregon, and Washington.

Most *C. mali* collections occurred in May, June, and July with few specimens collected in March, April, and August. The collections of *C. mali* peaked sharply in May, June, and July, indicating a relatively smaller phenological window for adult flight. *Chrysobothris mali* was thoroughly sampled across the Pacific Coast states, and the shorter window for peak activity is not due to a lack of sampling in central and southern California where we would expect to see adult flight period extended. One *C. mali* was collected in January in Napa, California and this collection date is assumed to be an error. No other *Chrysobothris* specimens were collected in January or February.

Table 4. A list of all plant associations on *Chrysobothris mali* museum specimen labels

Family	Common name	Plant species	No. observations	Association type
Asteraceae	Rabbitbrush	*Chrysothamnus* sp.	1	ns (1)
Betulaceae	Alder	*Alnus* sp.	1	Beating (1)
Ericaceae	Pacific madrone	*Arbutus menziesii* Pursh.	1	ns (1)
Ericaceae	Hoary manzanita	*Arctostaphylos canescens* Eastw.	4	Beating (4)
Ericaceae	Manzanita	*Arctostaphylos* sp.	2	ns (2)
Ericaceae	Whiteleaf manzanita	*Arctostaphylos viscida* Parry	6	Beating (5); flying to (1)
Fagaceae	California live oak	*Quercus agrifolia* Née	1	ns (1)
Fagaceae	Gambel oak	*Quercus gambelii* Nutt.	1	Beating (1)
Fagaceae	Oak	*Quercus* sp.	1	Reared (1)
Glossulariaceae	**Crater Lake currant**	***Ribes erythrocarpum* Coville & Leiberg**	**12**	**Reared (12)**
Juglandaceae	Walnut	*Juglans* sp.	1	ns (1)
Pinaceae	Pacific silver fir	*Abies amabilis* Doug. Ex J. Forbes	1	'From logs' (1)
Pinaceae	Sugar pine	*Pinus lambertiana* Doug.	2	Flying to (2)
Pinaceae	Singleleaf pinyon	*Pinus monophylla* Torr. & Frém.	1	On (1)
Pinaceae	Ponderosa pine	*Pinus ponderosa* Doug. Ex P. Lawson & C. Lawson	1	Flying to (1)
Pinaceae	Douglas fir	*Pseudotsuga menziesii* (Mirb.) Franco	1	On logs (1)
Platanaceae	California sycamore	*Platanus racemosa* Nutt.	3	Cut from (3)
Rhamnaceae	Buckbrush	*Ceanothus cuneatus* (Hook.) Nutt.	49	Beating (35); reared (2); flying to (4); ns (8)
Rhamnaceae	Sandscrub Ceanothus	*Ceanothus dentatus* Torr. & A. Gray	1	ns (1)
Rhamnaceae	Desert Ceanothus	*Ceanothus greggii* var. *perplexans* (Trel.) Jeps.	1	Beating (1)
Rhamnaceae	Deerbrush	*Ceanothus integerrimus* Hook. & Arn	1	Beating (1)
Rhamnaceae	Lemmon's Ceanothus	*Ceanothus lemmonii* Parry	1	Flying to (1)
Rhamnaceae	Prostrate Ceanothus	*Ceanothus prostratus* Benth.	3	Near (3)
Rhamnaceae		*Ceanothus* sp.	3	ns (2); reared (1)
Rhamnaceae	Snowbush	*Ceanothus velutinus* Doug. Ex Hook.	4	Beating (4)
Rosaceae	Taiwanese photinia	*Photinia serratifolia* (Desf.) Kalkm	1	ns (1)
Rosaceae	Pacific serviceberry	*Amelanchier alnifolia* (Hook.) Nutt.	2	Beating (1)
Rosaceae	**Common serviceberry**	***Amelanchier arborea* (F. Michx.) Fernald**	**8**	**Beating (1); flying to (1); reared (6)**
Rosaceae	Serviceberry	*Amelanchier* sp.	8	Beating (1); flying to (7)
Rosaceae	birch-leaf mountain-mahogany	*Cercocarpus betuloides* Nutt	12	ns (12)
Rosaceae	**Curl-leaf mountain-mahogany**	***Cercocarpus ledifolius* Nutt.**	**2**	**Reared (1); ns (1)**
Rosaceae	Alderleaf cercocarpus	*Cercocarpus montanus* Raf.	5	Beating (5)
Rosaceae	Mountain mahogany	*Cercocarpus* sp.	14	ns (11); On (2); beating (1)
Family	Common name	Plant species	No. observations	Association type
Rosaceae	River hawthorn	*Crataegus douglasii* Lindl.	1	ns (1)
Rosaceae	Hawthorn	*Crataegus* sp.	3	ns (1); trapped on (2)
Rosaceae	Apple	*Malus domestica* Mill.	2	ns (2)
Rosaceae	Sweet cherry	*Prunus avium* L.	3	ns (1); on (2)
Rosaceae	Bitter cherry	*Prunus emarginata* (Douglas) Eaton	1	On (1)
Rosaceae	Desert apricot	*Prunus fremontii* Watson	1	ns (1)
Rosaceae	Peach	*Prunus persica* (L.) Batsch	12	ns (12)
Rosaceae	Plum	*Prunus* sp.	10	Flying to (1); ns (8); on (1)
Rosaceae	chokecherry	*Prunus virginiana* L.	2	ns (2)
Rosaceae	Mexican cliffrose	*Purshia mexicana var. stansburyana* (Torr.) Welsh	1	ns (1)
Salicaceae	Pacific willow	*Salix lasiandra* Benth.	3	Beating (3)
Salicaceae	Arroyo willow	*Salix lasiolepis* Benth.	4	ns (4)
Salicaceae	Willow	*Salix* sp.	4	Beating (2); on (2)
Sapindaceae	Norway maple	*Acer platanoides* L.	1	On (1)

Bold rows indicate new species records for *Chrysobothris mali*.

The collection activity was often noted by the collector. "Beating" indicates collection via beat sheet. Adult specimens labeled with "reared" or "cut from" were considered to indicate reproductive host associations. The label "ns" indicates the collector did not specify the association type.

Information regarding the phenology of *C. femorata* and *C. mali* is limited and is geographically restricted. Maxwell (1935) found peak emergence of *C. femorata* occurs in May in Oklahoma, while Fenton (1937) found the vast majority *of C. femorata* emerged in June. However, the validity of the Maxwell (1935) and Fenton (1937) phenology results is complicated by the Wellso and Manley (2007) revision of the *C. femorata* species complex. All work with *C. femorata* before the revision is therefore subject to some taxonomic uncertainty. Despite the uncertainty, our phenology results created using Pacific Coast *C. femorata* specimens align with the observations of Maxwell (1935) and Fenton (1937). The *C. mali* phenology results are consistent with Burke and Böving (1929), who stated that the majority of *C. mali* adults emerged in June and July in Placerville, California. Many of the *C. mali* specimens analyzed in this study were collected from the Central Valley of California in the early 20th century, further supporting the Burke and Böving (1929) findings.

Morphological measurements and sex determinations were completed for the specimens from MTJM, WFBM, ODA, and OSAC collections. The results from these exploratory measurements indicate that average *C. mali* size is significantly smaller than *C. femorata* size, and the average male of both species is significantly smaller than the average female. Although the species and sexes differed in size, there was a considerable amount of overlap in the size distributions for all comparisons (Fig. 2). Consequently, size is not a valuable predictor in determining sex or species. However, data on adult borer body size may relate to host plant size or the number of larvae utilizing a single host tree. Both species use a wide array of deciduous woody plants for development and have been reported to develop inside thin currant branches, as well as thick scaffold branches of mature walnut trees (Burke and Böving 1929, Rijal 2020). There may be a relationship between the size of the adult beetle and the size or diameter of the host plant resource in which the larvae complete their development. Utilization of different hosts in these two species could also indicate specialization and may affect the ratio of *C. mali* and *C. femorata* found in the western United States, as well as the impacts of each species on the agricultural industry. The relationship between adult beetle body size and host plant use should be investigated in future work with these species.

Chrysobothris mali was strongly associated with Rosaceae in the genera *Amelanchier*, *Cercocarpus*, and *Prunus*, as well as *Ceanothus* (Rhamnaceae), and the species *R. erythrocarpum* (Glossulariaceae) (Table 4, Fig. 6). The affinity of *C. mali* for plants in the family Rosaceae was documented by Burke (1917, 1919) and Burke and Böving (1929). Because many important fruit, nut, and berry agricultural crops are in the family Rosaceae, as well as cultivated roses, the *C. mali* affinity for Rosaceae elevates the risk of *C. mali* damage to agricultural crops. Interestingly, the families Betulaceae and Juglandaceae only appear once in the associated plant list for *C. mali*, despite the historic presence of cultivated hazelnuts and walnuts within their range (Fig. 5; Table 4). Industry expansion and climate change have likely led to the increase in flatheaded borer damage to cultivated hazelnuts and walnuts in the western United States. Newly planted orchards are vulnerable to extreme weather conditions, thus providing ample host resources regardless of whether they represent preferred hosts.

Chrysobothris femorata is strongly associated with the genera *Betula*, *Populus*, and *Quercus*, indicating a strong relationship with the families Betulaceae, Salicaceae, and Fagaceae, respectively (Figs. 5 and 6; Table 3). Trees belonging to these families are grown commercially and transplanted as ornamental plants. There was a notable lack of associations with maple (*Acer* spp.) in the *C. femorata* specimen data, as the *C. femorata* affinity for *Acer* spp. has become a management challenge in nurseries in the eastern United States (Oliver et al. 2010, Seagraves et al. 2013, Dawadi et al. 2019, Addesso et al. 2020).

The plant associations of the two species did not overlap often; out of the 50 associated plant taxa, only four associations were shared between the species. Both species were associated with *M. domestica, Pl. racemosa*, *Pr. avium,* and *S. lasiandra.* The apparent lack of overlap in plant resource use between the two species may indicate host or niche specializations. Generally, the plants that *C. mali* are associated with have shrubby or small growth habits, while many

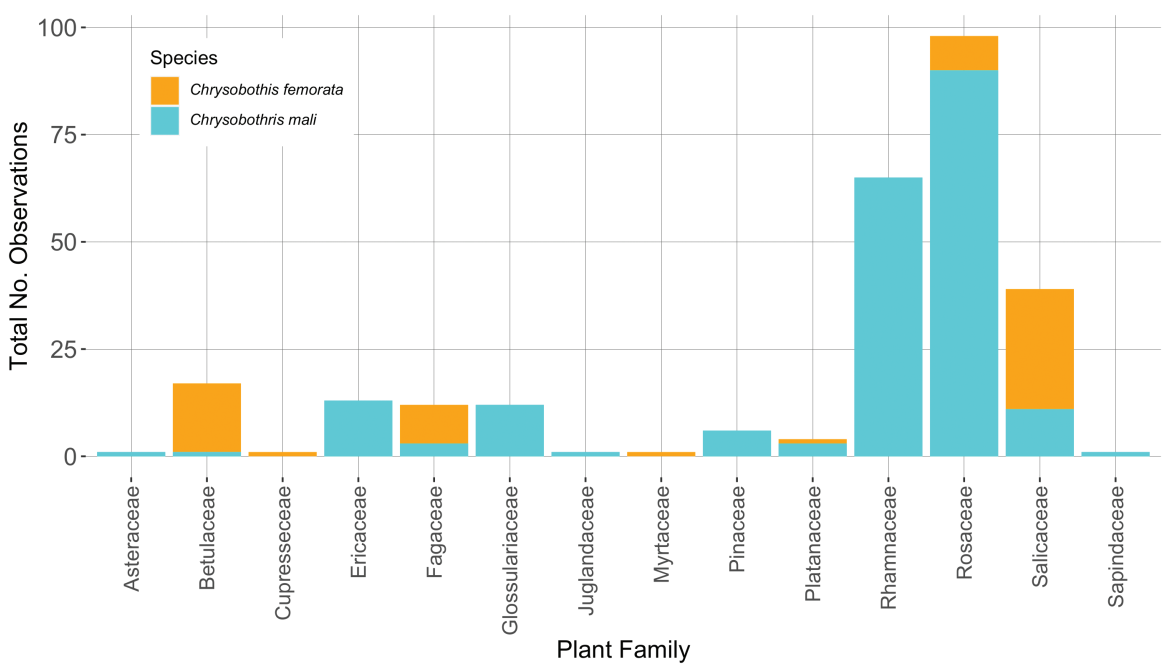

Fig. 5. A stacked histogram of the plant families associated with each species. Associations are not limited to reproductive hosts.

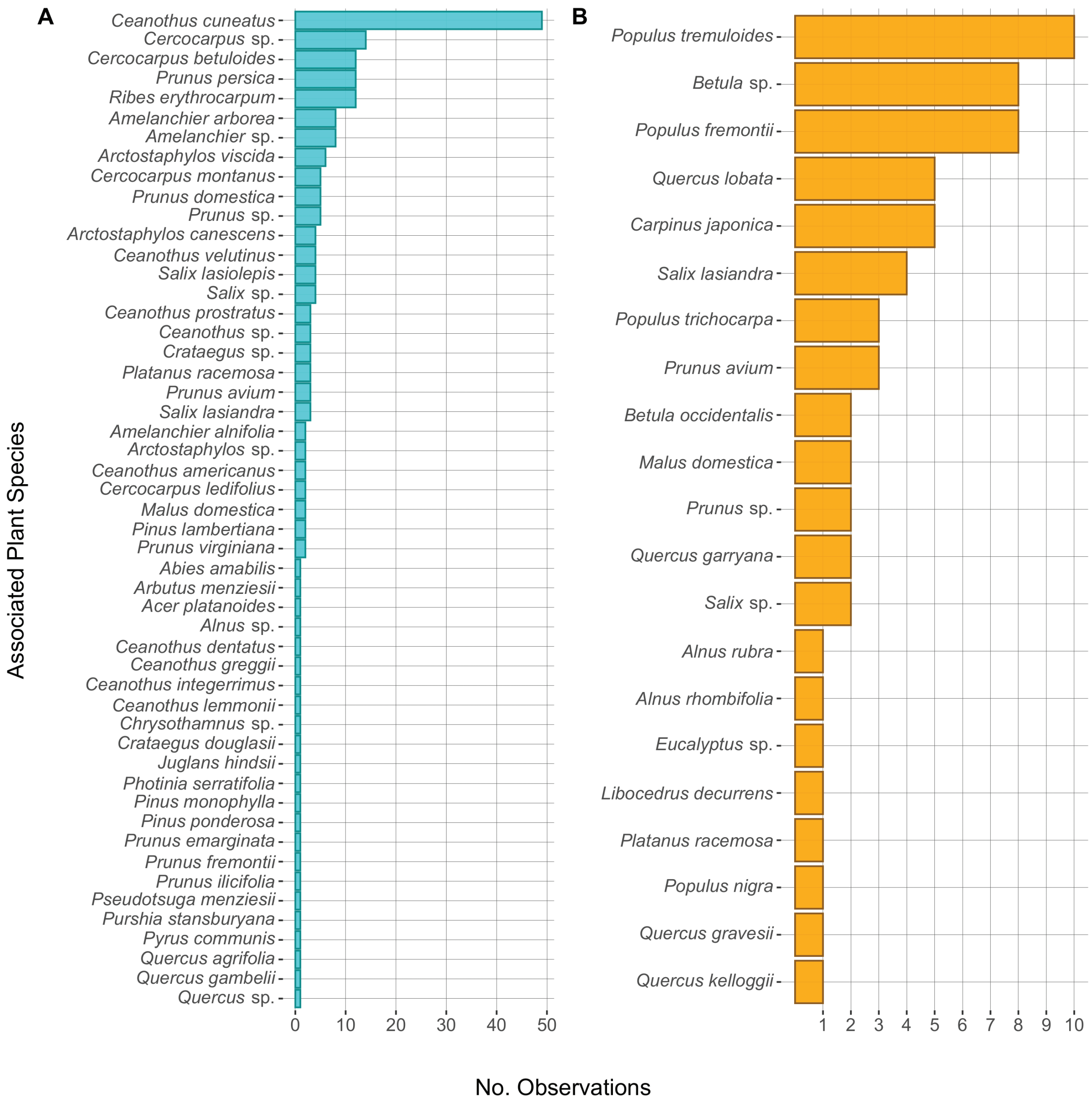

Fig. 6. Rank and abundance histograms of the various plant species associated with Chrysobothris mali (A) and *Chrysobothris femorata* (B). Associations are not limited to reproductive hosts.

of the *C. femorata* plants are large trees. *Chrysobothris femorata* was larger than *C. mali* in our analyses and this body size and tree size association could be related to their host specializations. Future studies should investigate whether these two variables are related.

Reared associations are needed to determine whether a plant can be used as a reproductive host for either *C. mali* or *C. femorata*. However, apart from a few infrequent coniferous tree associations, the other plant association records provide valuable information as to potential reproductive hosts. Most of the plant taxa are deciduous trees and belong to genera that have been documented as reproductive hosts. Given the highly polyphagous nature of these species, it is likely the adult beetles are using some of these woody, deciduous plants as hosts for reproduction. Additionally, several of the associated plant species have appeared on previously published host lists for *C. femorata* and *C. mali* (Fig. 6; Tables 3 and 4). The frequency with which adult beetles were collected on certain plant species indicates the strength of the relationship. For example, *C. femorata* was collected on *Po. tremuloides* 10 times but collectors did not indicate that they reared the specimen from *Po. tremuloides* material. *Populus tremuloides* is a known reproductive host for *C. femorata*, as are many of the other plants associated with *C. femorata* at high frequencies. Inference aside, the plant association data provide researchers with clues about *C. mali* and *C. femorata* ecology in natural environments where their habits are poorly understood. Host association information can be valuable to collectors and can be important for pest management where commercial tree crops may be affected by immigrating *Chrysobothris* spp. from surrounding vegetation.

The sampling of host plants and associated plant species could be biased by the collector. To find valid hosts, the collector must rear adult beetles from infested wood samples. Buprestid rearing requires specialized knowledge of flatheaded borer biology, so it is not surprising that few collectors take the time to rear beetles from infested wood. The collectors may have prior experience finding either species in or on a certain plant. Previous host knowledge would lead the collector to target those specific plants for the maximum chance of finding beetles; thus, potentially missing novel hosts that would be found through random sampling. However, this random sampling approach is time consuming, and one would have to be purposefully looking for new hosts instead of simply trying to find beetles.

Another source of collection bias is the date range in which these specimens were collected. Median collection years were between 1923 and 1969, with a notable gap in the sampling effort from 1971 onward. Thus, the data reflect the distributions and phenology of the two species around the middle of the twentieth century. It is possible that climate-change-induced range and phenological shifts have occurred in the two species over the last 50+ yrs, as evidence of these shifts have been seen in other taxa (Karban and Strauss 2004, Kelly and Goulden 2008). Consistent and targeted taxon sampling can reduce this type of bias (Graham et al. 2004).

Although the historic nature of these collections represents a source of bias, these data also provide the researcher with the opportunity to step into the past to work with entomologists and insect enthusiasts who played a part in shaping the field of entomology today. Specimens pinned by many of the first entomologists to work on the Pacific Coast are housed in these collections. Early entomologists such as Harry E. Burke, Edwin Van Dyke, and Melville Hatch contributed flatheaded borer specimens to these collections in the early 1900s and entomologists are still able to benefit from their work 100 yrs later. Individuals such as Frank M. Beer and William F. Barr were avid collectors, contributing 139 and 43 specimens, respectively between the years 1939–1984. The sampling efforts of Buprestid expert, Rick Westcott, contributed to 64% of the total specimens housed in the *C. femorata* and *C. mali* collections at the ODA (i.e., [n = 105] of 163 specimens). These avid collectors raised the median collection year of the WFBM and the ODA collection by 20–40 yr when compared to the other museums (Fig. 1; Table 1). Their efforts and subsequent gaps highlight the need for ongoing sampling and contributions of specimens to natural history museums. The gap in sampling effort after 1971 is concerning. It is important to continue efforts to tangibly document Earth's biodiversity so baselines of diversity, community composition, and the basic biology of various insects can be compared with past data and applied to answer future research questions (Graham et al. 2004, Chapman 2005, Baird 2010).

Supplementary material

Supplementary material are available at *Annals of the Entomological Society of America* online.

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Author Contributions

Erica Rudolph (Conceptualization-Equal, Data curation-Lead, Formal analysis-Lead, Methodology-Lead, Writing – original draft-Lead), Nik Wiman (Conceptualization-Equal, Formal analysis-Supporting, Funding acquisition-Lead, Methodology-Supporting, Writing – review & editing-Supporting)

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