Greater horseshoe bats and their insect prey: the impact and importance of climate change and agri-environment schemes

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Project Head: Professor Gareth Jones[1], Gareth.Jones@bristol.ac.uk

Co-supervisor: Dr Kate Barlow[2], KBarlow@bats.org.uk

Research collaborator: Dr Roger Ransome[1], rogerransome@hotmail.com

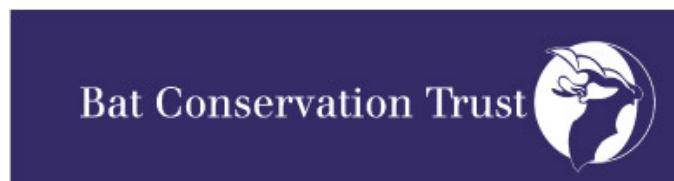*Research assistant: Lia Gilmour[1] Lia.Gilmour@bristol.ac.uk*

[1] School of Biological Sciences, University of Bristol

[2]Bat Conservation Trust

Executive summary

- Climate warming over the last few decades has led to phenological shifts for many species and is predicted to continue affecting biodiversity worldwide under certain climate projections (IPCC, 2014).

- We have analysed phenological changes in diets of greater horseshoe bats (*Rhinolophus ferrumequinum*) by microscopic analysis of faecal samples collected from Woodchester Mansion between 1968 and 2012 to determine trends in the phenology of important prey species in the diet, and investigated whether diet phenology was related to summer roost counts and birth timing.

- Analysis of timings of appearance (peak and first appearance) for key prey in diet between 1969-2012 showed that the peaks in dietary composition for cockchafers (*Melolontha melolontha*) and crane flies (Tipulidae) eaten during the spring have advanced significantly despite considerable year-to-year variation.

- Long-term study of this colony by Dr R. D. Ransome shows that mean date of birth of pups is also getting significantly earlier for greater horseshoe bats at this site.

- We therefore tested the hypothesis that the timing of births is positively correlated with the appearance of key prey items in the diet in spring, and found significant positive correlations between mean date of birth and timing of peak and first appearance of cockchafers in the diet, and with timing of peak appearance of springtime tipulids. We discuss the possibility and implications of both prey availability and bat birth timing being driven by long-term changes in climate.

- Changes in mean percentage dietary volume of key prey groups (moths, *Aphodius* beetles and *M. melolontha*) are also analysed. Moths have decreased in the diet of bats at Woodchester since 1969, and *Aphodius* and *M. melolontha* have increased. Moth trends may be related to changes in moth populations over time and *Aphodius* increases may be in part due to habitat management under agri-environment schemes. It is uncertain why *M. melolontha* have increased in bats' diets over time.

- Our results have implications for greater horseshoe bat conservation, as continuing shifts in diet phenology due to climate or habitat management may affect the future survival of maternity colonies including the one studied here.

- Ongoing work will include a comparison of morphological dietary analyses presented here with those from molecular analyses over same time period (in collaboration with Kristine Bohmann at the University of Copenhagen). Comparison with molecular findings is important as will allow us to look at changes in diversity of some key prey groups (e.g. moths, tipulids), over time.

- The next stages of work are to test the hypotheses that agri-environment schemes may benefit greater horseshoe bat populations by improving food availability, through field surveys and habitat mapping. This work is being carried out by Jérémy Froidevaux, PhD student who started October 2014, supervised by the Project Lead, Gareth Jones.

Introduction

During the last few decades, world temperatures have been significantly warmer and are predicted to rise further under future climate change projections, causing shifts in weather systems and sea level rises (IPCC, 2014). Climate change has already led to phenological shifts in many taxa, has caused biodiversity declines and continues to threaten global species populations on a large scale (Walther *et al.*, 2002). For example, modelling under future climate scenarios indicates an effect on distributions of European bat species (Rebelo *et al.*, 2010). On a more local scale, warmer springs have been related to earlier egg laying in some bird species (e.g. Sanz, 2003; Pearce-Higgins, 2005) and earlier birth dates in greater horseshoe bats (*Rhinolophus ferrumequinum*) in southern Britain (Ransome & McOwat, 1994). Changes in the time of breeding may be linked to earlier emergence of key insect prey items (e.g. Pearce-Higgins, 2005), which are highly influenced by local climatic conditions such as temperature and humidity (e.g. Wagenhoff *et al.,* 2014). As a result of climate change, mismatching of timings of key prey emergence and the phenology of species eating those prey, could be a major determining factor in the future survival of many species, under certain climate scenarios (Visser & Both, 2005).

The intensification of agriculture has also contributed to biodiversity declines in a wide range of taxa over the past 50 years in the UK and other parts of northern Europe (Krebs *et al.*, 1999; Robinson & Sutherland 2002). Agricultural landscapes are especially important for biodiversity, as they comprise about three-quarters of the UK's land area (Defra, 2008). Agri-environment schemes represent one way of balancing the negative impacts of agricultural development by maintaining and encouraging biodiversity. Under agri-environment schemes, landowners are paid to enhance habitats in areas where threatened species occur. Evidence for whether these schemes are successful is lacking.

One often-quoted success story involves how agri-environment schemes may have promoted population growth in greater horseshoe bat populations (e.g. Longley, 2003; Maclean, 2010; RSPB, 2013). Ecological data collected Roger Ransome and colleagues at the University of Bristol were used to suggest appropriate habitat management to assist with the conservation of the species under the Species Recovery Program (SRP) and then later the Countryside Stewardship Scheme (CSS) (Ransome, 1996; Duvergé & Jones, 2003). Land managers who maintained land close to maternity colonies were encouraged to apply for grant aid through CSS administered by the Department for Environment, Food and Rural Affairs (Defra). The National Bat Monitoring Programme (NBMP) has collected data on numbers of bats in summer maternity roosts of greater horseshoe bats since 1997 (BCT, 2013, 2015; Barlow *et al.*, 2015). There has been a significant upward trend in the count data with an overall increase of 109% since the base year (1999). Although some of this increase may be due to climate change, the success of CSS may have made a major contribution to the impressive increase in numbers of a flagship conservation species (Longley, 2003; RSPB, 2013). More recently the guidelines developed under CSS have been absorbed into Higher-Level Stewardship schemes, and the enhancement protocols around greater horseshoe bat maternity colonies continue to be implemented. The greater horseshoe bat is one of five mammal species that will receive bespoke management recommendations under new Countryside Stewardship schemes opening in 2015.

The greater horseshoe bat, one of the larger British bat species, is at the northern edge of its range in Britain with a distribution confined to south Wales and south west England (Aulagnier *et al.*, 2008; JNCC, 2013). Although the species is listed as *Least Concern* on the IUCN red list (Aulagnier *et al.*, 2008), it is locally threatened in Britain and protected under the UK Biodiversity framework, as well as being listed on Annex IV and II of the European Commission Habitats Directive (JNCC, 1992, 2013; JNCC & Defra, 2012). Eight Special Areas of Conservation (SACs) are listed with this species as a primary feature of site qualification and three are listed where it is a qualifying feature. The majority of major maternity roosts and hibernacula are listed as Sites of Special Scientific Interest (SSSIs), including the maternity roost at Woodchester Mansion, Gloucestershire, the focus of this project.

Woodchester Mansion is an unfinished gothic revival mansion house, surrounded by parkland, woodland and grazed pasture and is an important maternity colony for greater horseshoe bats in the area. The colony has been studied extensively by Dr Roger Ransome and colleagues for over 50 years and long-term data have been collected including colony statistics such as births and deaths, as well as diet data (e.g. Ransome & McOwat, 1994; Ransome, 1996; 1997; 2000). As part of this long-term study, faeces have been collected from underneath the colony on a weekly basis since 1968. Data collected over such a long period is a valuable resource for studying changes in diet phenology and this can be related to changes in climate, agricultural practices and other external factors that may affect a colony of bats.

Greater horseshoe bats are highly selective in choosing their prey, conforming to optimal foraging models and only selecting lower quality prey (Diptera and Ichneumonidae), when higher quality items (*Melolontha melolontha* and Lepidoptera) are scarce (Jones, 1990; Ransome, 1996; 1997; 2000). *Aphodius* beetles are also an important food source for juvenile bats during the development of flight and hunting skills in summer and early autumn and can be important for lactating mothers when moths are scarce (Ransome, 1996; 2000; Duvergé & Jones, 2003). Colonies are dependent on a habitat that supports these prey, as well as the other groups mentioned (Ransome, 1996; 1997; 2000; Duvergé & Jones, 2003). Both the topography of the habitat surrounding a roost and how it is managed are important in determining the availability of certain prey groups (Ransome, 1996; 1997; 2000; Duvergé & Jones, 2003). Appropriate management is thought to be highly important for colony survival and growth (Ransome, 1996, 2000; Duvergé & Jones, 2003). For example, suitable cattle grazing regimes provides food for *Aphodius* and *Geotrupes* dung beetles, which are key prey groups for the bats at different times in the year (Ransome, 1996; 1997; 2000; Longley, 2003). Weather conditions and climate also affect the availability of insect prey species and changes in climate at key timings (e.g. spring) could subsequently affect birth timings in greater horseshoe bats (e.g. Pearce-Higgins, 2005).

In summary, for effective conservation of greater horseshoe bats long-term, it is important to investigate their diet phenology and whether climate and/or habitat management are influencing changes in colony size. Key objectives of this project and future projects are therefore as follows:

Objectives

Has the phenology of key prey items of greater horseshoe bats changed over the past 45 years?

We have extracted subsamples of droppings collected weekly by Roger Ransome (Project Collaborator) at the greater horseshoe maternity colony at Woodchester Mansion since 1968, allowing us to analyse phenological changes in diet from this site 1969-2012.

Are key prey items appearing earlier in the diets of greater horseshoe bats at Woodchester Mansion and is this related to changes in birth timings since 1969? Is this related to climate?

We have analysed timings of appearance (first and peak) of cockchafers (*Melolontha melolontha*) and crane flies (Tipulidae) in the diets of greater horseshoe bats at Woodchester Mansion and related results to mean dates of birth for the colony. Earlier births and correlated appearances of cockchafers and tipulids are likely to be related to changes in climate over the last four decades.

Has the abundance of key prey items in greater horseshoe bats at Woodchester Mansion changed over time since 1969?

We have analysed the change in abundance of moths (Lepidoptera), cockchafers (*M. melolontha*) and *Aphodius* beetles over selected years between 1969 to 2012. Changes in key prey items in the diet of bats are likely to be due to general documented declines of some species in the UK (in the case of moths) and the positive effect of implemented agri-environment schemes (in the case of *Aphodius*).

Work completed

- Analysis of droppings from subsamples of sixteen selected years between 1969 and 2012.
- Analysis of timings of key prey appearance (first and peak appearances) in diet over time (1969-2012) to test the hypothesis that key prey are appearing earlier in the diet.
- Analysis of whether trends in the size of the maternity colony can be related to diet phenology.
- Relate peak timing of key prey abundance in diet to mean birth date. Test the hypothesis that the timing of birth is positively associated with the appearance of key prey items in the diet, and determine if both are driven by long-term changes in climate.

Work to complete

- Compare results from morphological dietary analyses presented here with those from molecular analyses over same time period, performed by Kristine Bohmann (KB), University of Copenhagen, co-supervised by Gareth Jones (GJ). *Complete by end mid-2015 and results from PTES project will be related to KB's findings due then.*

- Set up logistics of field surveys and GIS mapping at greater horseshoe bat maternity sites under agri-environment schemes to be performed by Jérémy Froidevaux, PhD student starting October 2014. Relate findings to NBMP data on colony growth. Although this was originally in the project objectives, GJ obtained funding for it to be performed under a studentship from the BBSRC. With agreement from PTES, we therefore expanded the dietary phenology aspects of the study. *The agri-environment scheme aspects will be completed by end August 2018, as work will be performed under the BBSRC studentship.*

Methods

Microscopic analysis

We carried out microscopic analysis of key prey items extracted from subsamples of greater horseshoe bat droppings collected weekly by Roger Ransome (Project Collaborator) at a maternity colony at Woodchester Mansion since 1968. We analysed phenological changes of key prey items and related results to changes in mean date of birth data for the colony. Changes in numbers of bats in the colony over time were also analysed. Dates of birth and numbers of births were recorded by Roger Ransome from 1969 to 2012, as part of a long-term study on the bats at this site (e.g. Ransome & McOwat, 1994; Ransome, 1996; 1997; 2000). Colony count data was provided by Roger Ransome towards the Bat Conservation Trust's (BCT) National Bat Monitoring Program (NBMP: BCT, 2013; 2015; Barlow *et al.*, 2015).

12 droppings were analysed from each weekly sample, from April to September for 16 years, between 1969-2012 (including eight years from 1999-2012 for which we have NBMP data showing change in roost size). Years analysed comprised 1969, 1972, 1977, 1980, 1987, 1990, 1995, 1999, 2001, 2006, 2007, 2008, 2009, 2010, 2011 and 2012. For each dropping analysed, percentage total of each prey species/group was noted, for the following prey groups: cockchafers (*Melolontha melolontha*), crane flies (Tipulidae), *Aphodius* beetles, *Geotrupes* beetles, Ichneumonidae (Hymenoptera), moths (Lepidoptera), caddis flies (Trichoptera), small dipteran flies (Diptera) and unknown. Mean percentage total abundance of each prey group was calculated for the 12 droppings per weekly sample. Weeks are numbered from one to 26, with the first week in April noted as week one.

Analysis of phenological changes and birth data

We analysed phenological changes in key prey items in diet from this site throughout the active bat season in each year (April to September). Key prey groups analysed included *M. melolontha*, crane flies/tipulids (Tipulidae), *Aphodius* beetles, *Geotrupes* beetles, Ichneumonidae (Hymenoptera) and moths (Lepidoptera). Other groups were recorded in low numbers and were not analysed (e.g. small Diptera and caddis flies).

We also analysed changes in timings of key prey groups in more detail from this list. Specifically, first and peak appearance of *M. melolontha* in the diets of bats and changes in timings of spring and autumn peak appearance of tipulids were analysed. First appearance was noted as the first week the species/prey group appeared in the bats' diet, and peak appearance was noted as the week in which the highest mean percentage total of the species/prey group was recorded. Years were omitted in the case of missing data (three years for *M. melolontha* first appearance data, four for tipulid spring data and two for autumn data). We then compared changes in mean birth date of bats from 1969 to 2012, to diet phenology, including changes in timings of appearance of *M. melolontha* and Tipulidae. It was not possible to look at first appearance of tipulids, as the group tended to appear in bats' diets before the time window analysed (April-September). Trends in numbers and dates of births (1969-2012, collected by R. Ransome) and total colony counts (1995-2012, collected by R. Ransome as part of BCT NBMP) are also analysed.

We analysed changes in mean percentage total abundance of moths (Lepidoptera), dung beetles (*Aphodius*) and *M. melolontha* at key times in the bats' diets over time (May to August for Lepidoptera, July to August for *Aphodius* and mid-April to late June for *M. melolontha*). Years were not included in analysis if more than one week were missing in a key month (1969 was excluded for *M. melolontha*, *Aphodius* spp. and Lepidoptera analysis; 1980 and 1990 were also excluded for *M. melolontha* analysis).

Correlations were performed in R (v3.1.2) using the Hmisc package (v3.14-6, Harrell, 2014). Normal data were tested using Pearson's correlation and are presented as Pearson's correlation statistics (r values) with n and p values in Table 1, with variables tested and key findings for prey group or for birth data. Non-normal data were tested using Spearman's correlation and are presented as the r_s statistic.

Results

Diet phenology

Key prey items recorded in the diets of greater horseshoe bats at Woodchester Mansion from 1969-2012 included *M. melolontha*, moths, *Aphodius* beetles and tipulids (Appendix 1). *Geotrupes* beetles were also recorded in bats' diets in early spring and late autumn and ichneumonid wasps were recorded in relatively lower percentages throughout the year.

Key prey species phenology and birth data

Despite considerable year-to-year variation, mean date of birth of bats (recorded by R. Ransome) at this site has been getting significantly earlier since 1969 (Table 1; Figure 1) and number of births (recorded by R. Ransome) and colony counts (from Bat Conservation Trust (BCT) NBMP: BCT, 2013) have been increasing since 1989 and 1997 respectively, after a population crash in 1986 (Ransome & McOwat, 1994) (Figure 2). The timing of peak appearance of cockchafers (*M. melolontha*) in the diets of bats at Woodchester Mansion has

also been getting significantly earlier (Table 1; Figure 3), although there was no significant relationship found in first appearance of cockchafers over time (Figure 4). There is a significant positive relationship between the time when *M. melolontha* appear in the diet (first and peak appearance) and the mean birth date of the same year (Figures 5, 6).

The timing of peak abundance of crane flies (Tipulidae) in spring has also significantly advanced, and the autumn peak has been getting later (Figures 7, 8). There is a significant positive relationship between this spring peak in crane flies and mean date of birth of bats at the site in the same year (Figure 9).

Changes in abundance of key prey over time

The abundance (mean percentage total) of moths in the diet of bats at this site appears to have increased from 1969 until 1995, and declined since 1987, though no significant relationship was found over the whole time window analysed 1969-2012 (Table 1; Figure 10). The abundance of small dung beetles (*Aphodius*) in the bats' diets however has significantly increased over the time window analysed (Figure 11). *M. melolontha* has also been increasing in abundance the diet since 1995, though no significant relationship was found over the whole time window analysed (Figures 12).

Figures and Tables

Table 1. Variables tested, results and key findings for each prey group and for birth/colony data (ns= non-significant, DOB=date of birth).

| Prey group	Variables tested	Results	Key findings
M. melolontha	First appearance over time	ns	No change first appearance of *M. melolontha* over time
M. melolontha	Peak appearance over time	r_{s16} = -0.56, P < 0.05	Peak *M. melolontha* getting earlier
M. melolontha	Mean % abundance over time	ns	No change abundance of *M. melolontha* over time
M. melolontha	First appearance and mean birth date	r_{13} = 0.77, P < 0.01	*M. melolontha* first appearance and mean DOB related
M. melolontha	Peak appearance and mean birth date.	r_{16} = 0.75, P < 0.001	*M. melolontha* peak appearance and mean DOB related
Tipulidae	Peak appearance (s) over time	$r_{s\,13}$ = -0.59, P < 0.05	Spring tipulid peak getting earlier
Tipulidae	Peak appearance (autumn) over time	$r_{s\,14}$ = 0.56, P < 0.05	Autumn tipulid peak getting later
Tipulidae	Peak appearance (spring) and mean birth date	r_{12} = 0.59, P < 0.05	Peak tipulid appearance (spring) and mean DOB related
Aphodius	Mean % abundance over time	$r_{s\,15}$ = 0.68, P < 0.01	*Aphodius* increased in diet since 1969
Lepidoptera	Mean % abundance over time	ns	No change in abundance of moths in diet 1969-2012 but see text
NA	Mean date of birth over time	$r_{s\,33}$ = -0.42, P < 0.05	Mean DOB earlier since 1969
NA	Number of births over time	$r_{s\,33}$ = 0.41, P < 0.05	No. births increased since 1969
NA	Colony count over time	$r_{s\,11}$ = 0.99, P < 0.001	No of emerging adults increased over time
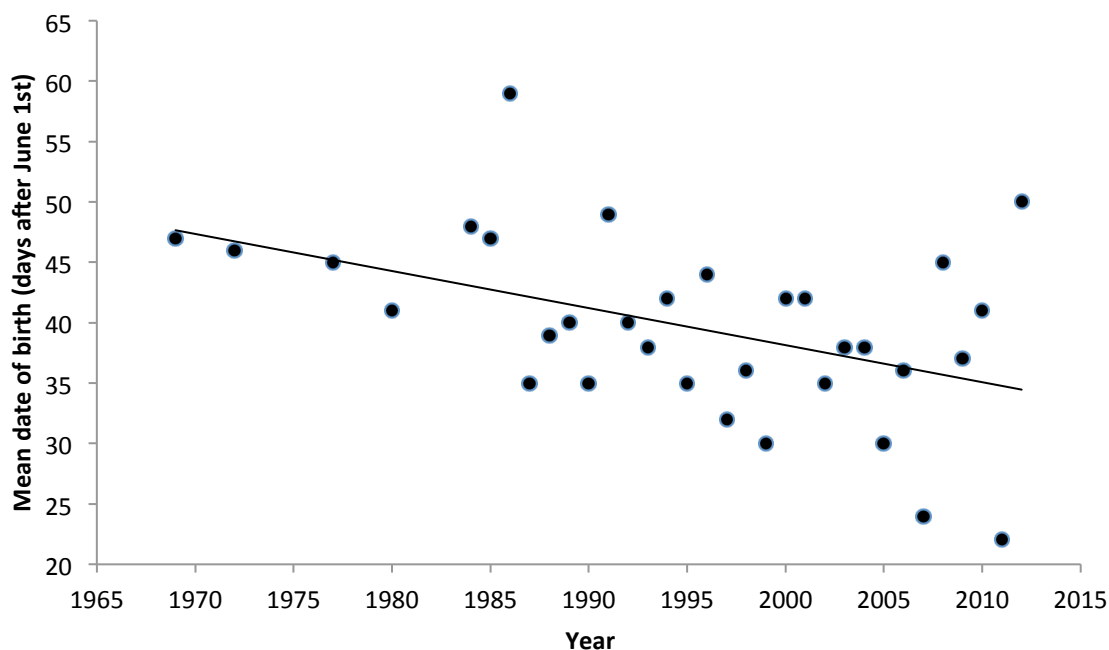
Figure 1. Changes in mean birth date of greater horseshoe bats at Woodchester Mansion 1969-2012. The negative correlation is statistically significant ($r_{s\,33}$ = -0.42, P < 0.05). Data from Roger Ransome.
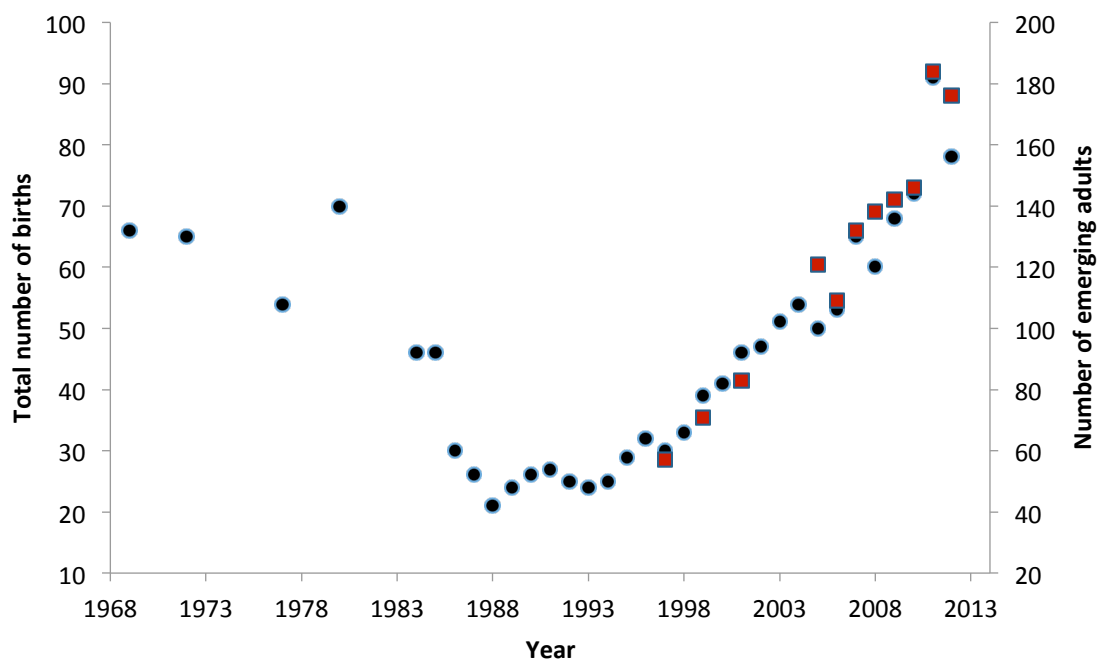

Figure 2. Changes in the total number of births (data from Roger Ransome, black dots) and total number of bats (red squares BCT NBMP data, collected by Roger Ransome) in a colony of greater horseshoe bats at Woodchester Mansion 1969-2012. Both positive correlations are statistically significant (births 1969-2012: $r_{s\,33}$ = 0.41, P < 0.05; colony count 1997-2012: $r_{s\,11}$ = 0.99, P < 0.001).
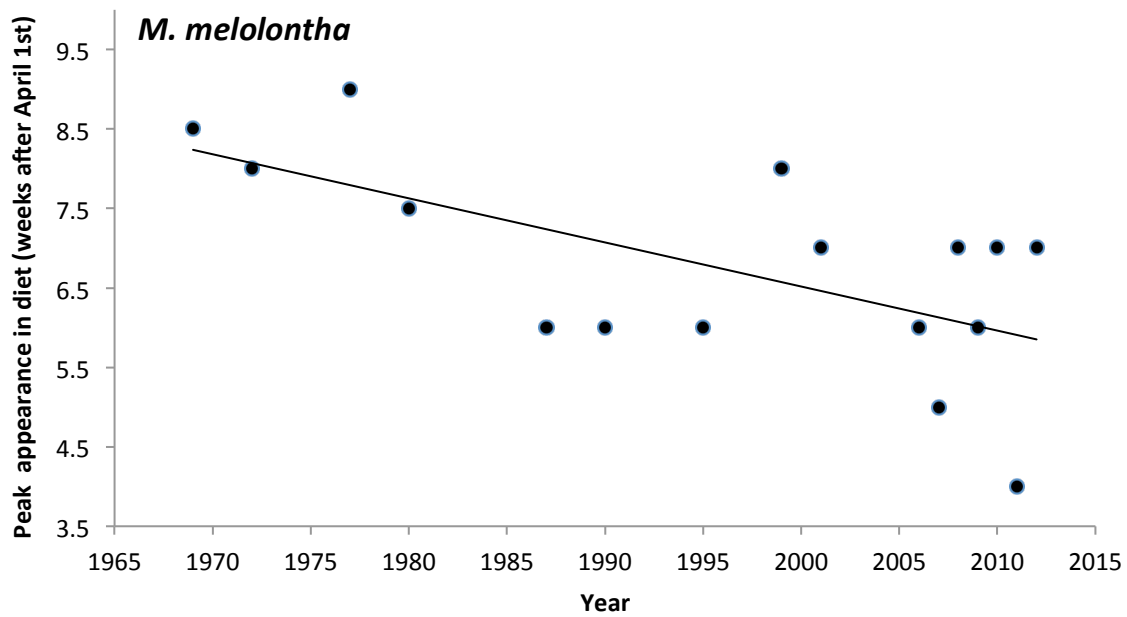
Figure 3. Changes in the time of peak appearance of cockchafers (*M. melolontha*) in the diets of Woodchester greater horseshoe bats 1969-2012. The negative correlation is statistically significant (r_{s16} = -0.56, P < 0.05).
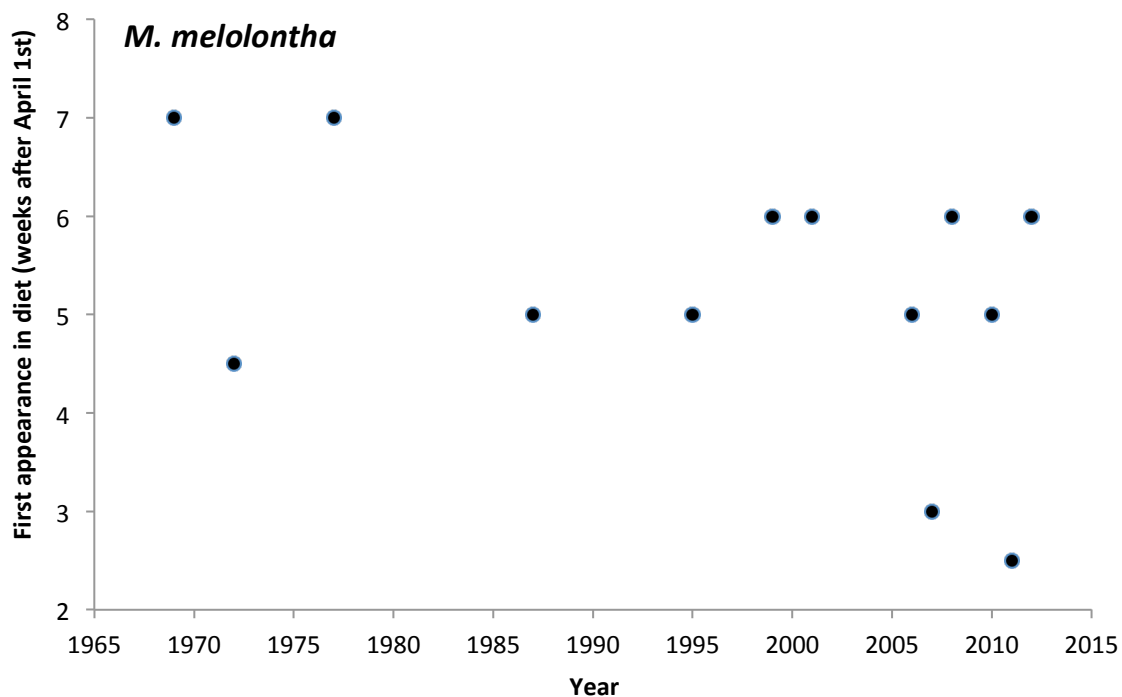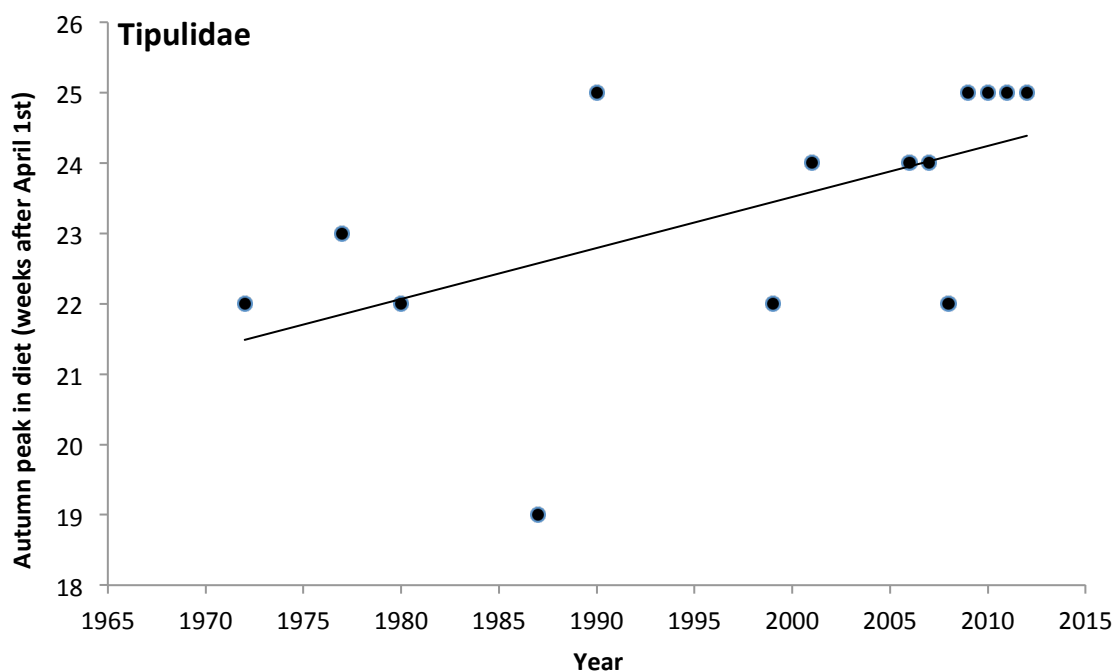

Figure 4. Changes in the time of first appearance of cockchafers (*M. melolontha*) in the diets of Woodchester greater horseshoe bats 1969-2012. The relationship is not statistically significant.
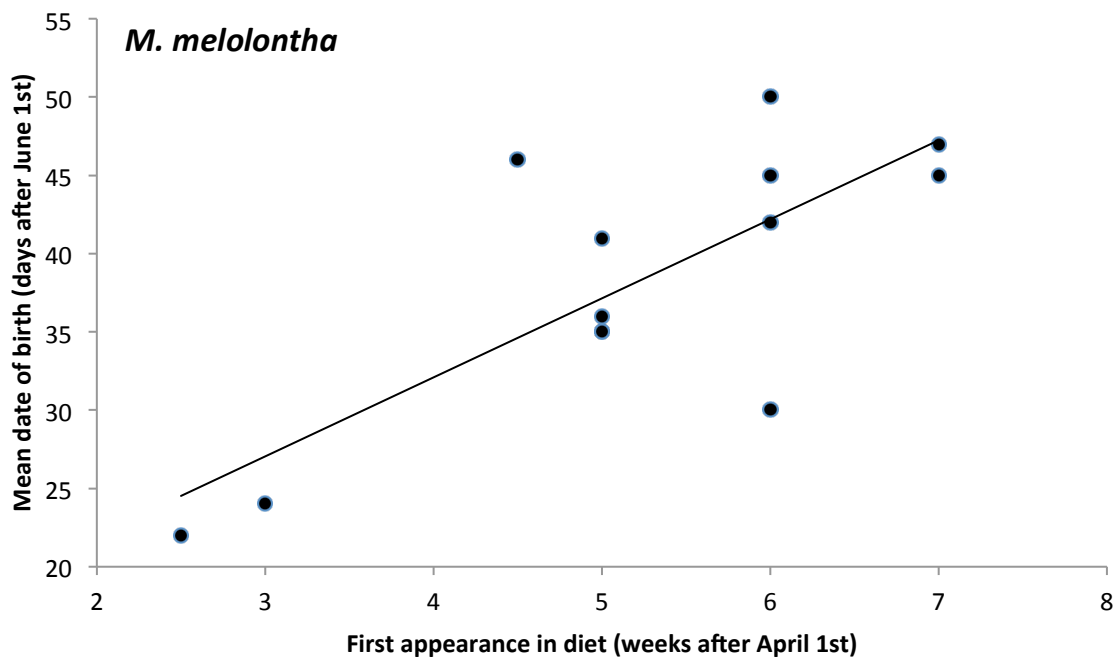
Figure 5. Relationship between mean birth date and date of first appearance of cockchafers in the diet of greater horseshoe bats at Woodchester Mansion 1969-2012. The positive correlation is statistically significant ($r_{13} = 0.77$; $P < 0.01$).
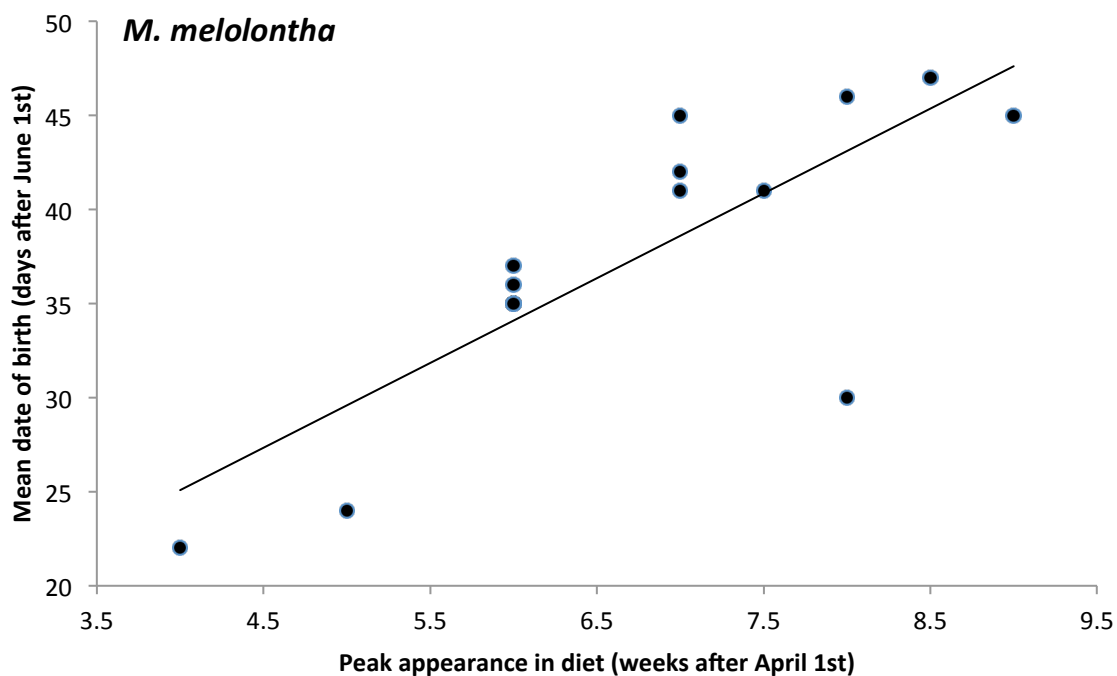
Figure 6. Relationship between mean birth date and date of peak appearance of cockchafers (*M. melolontha*) in the diet of greater horseshoe bats at Woodchester Mansion 1969-2012. The positive correlation is statistically significant ($r_{16} = 0.75$; $P < 0.001$).
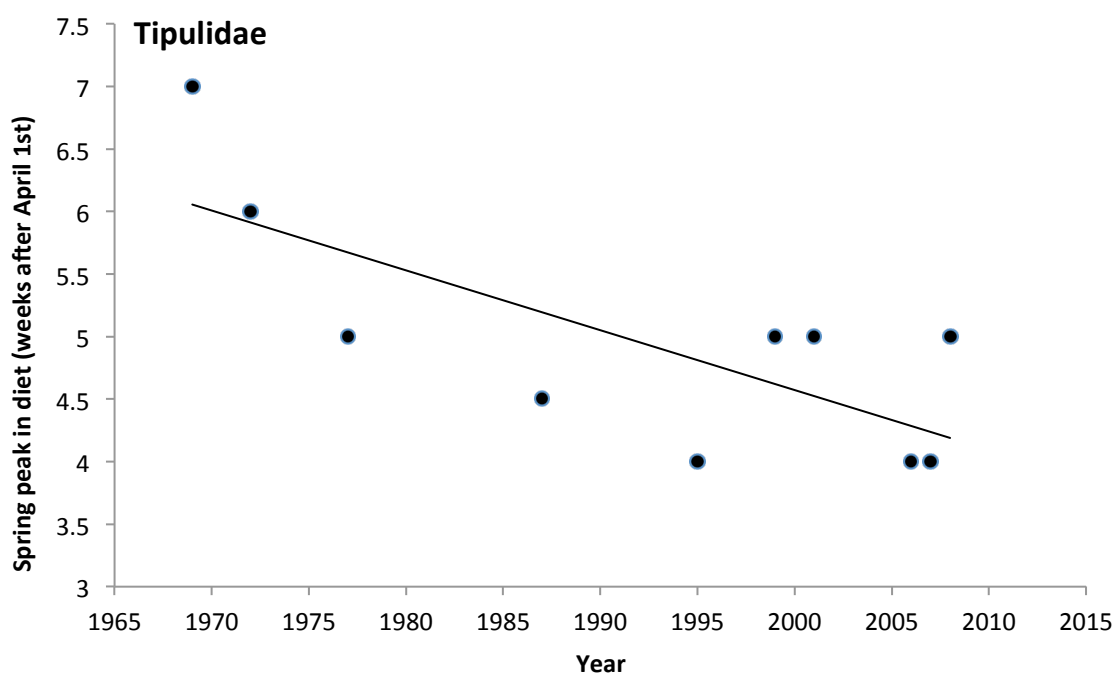
Figure 7. Changes in the time of peak spring appearance of crane flies (Tipulidae) in the diets of Woodchester greater horseshoe bats 1969-2012. The negative correlation is statistically significant ($r_{s\ 13}$ = -0.59, P < 0.05).
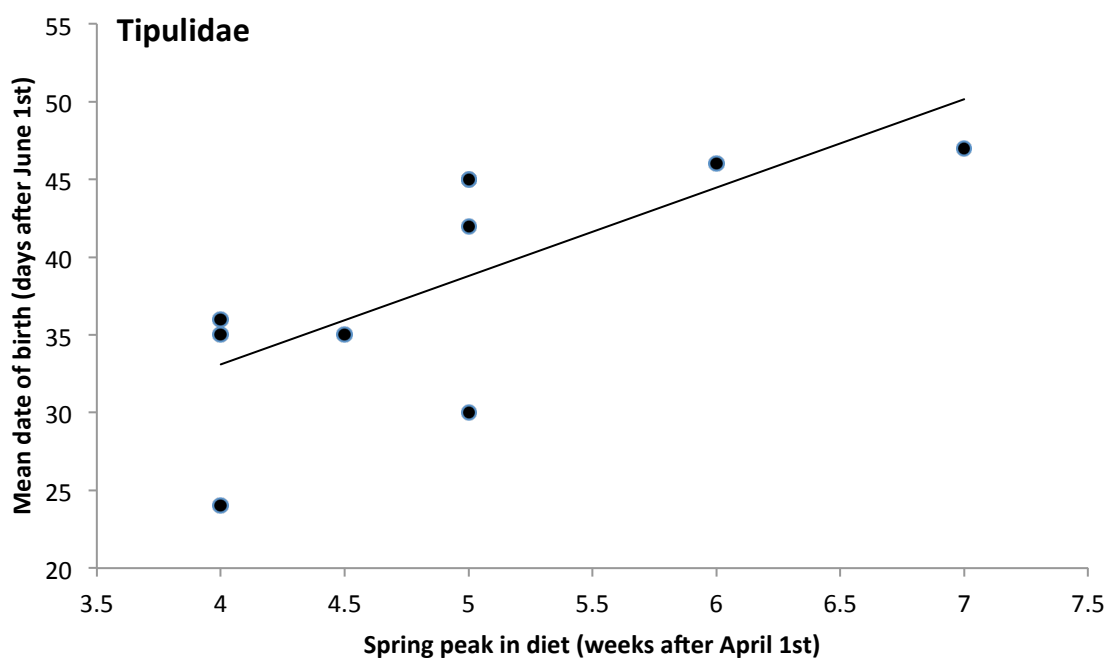

Figure 8. Changes in the time of peak autumn appearance of crane flies (Tipulidae) in the diets of Woodchester greater horseshoe bats 1969-2012. The positive correlation is statistically significant (r_{14} = 0.56; P < 0.05).

Figure 9. Relationship between mean birth date and date of spring peak appearance of crane flies (Tipulidae) in the diet of greater horseshoe bats at Woodchester Mansion 1969-2012. The positive correlation is statistically significant ($r_{12} = 0.59$; $P < 0.05$).
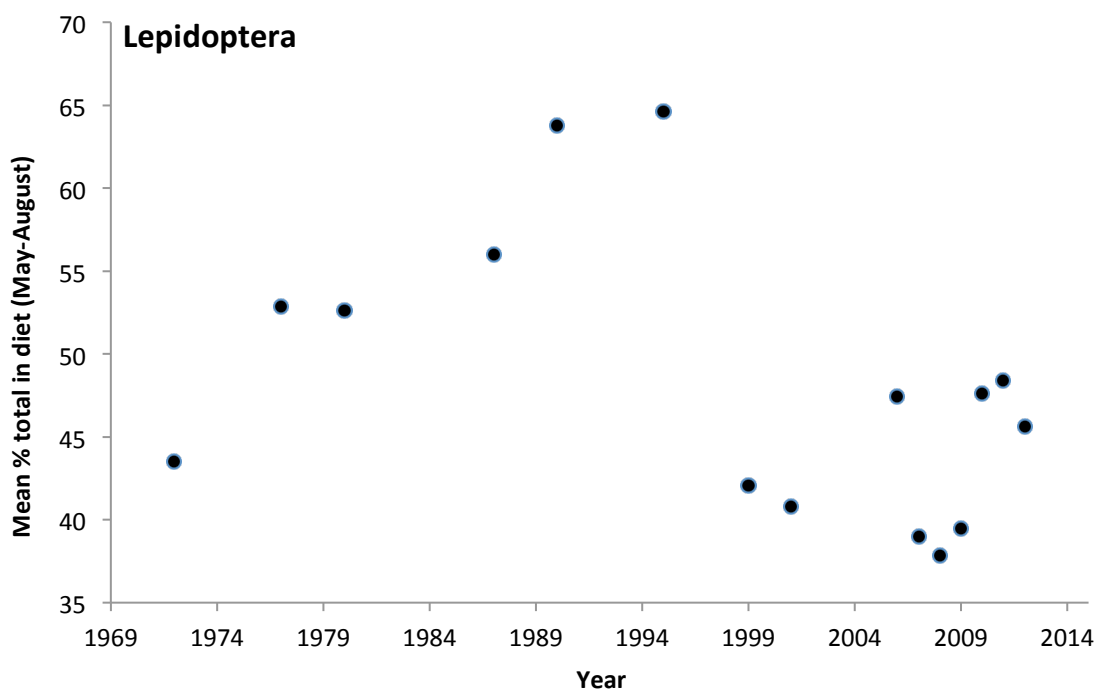

Figure 10. Changes in the abundance of Lepidoptera in the diets of Woodchester greater horseshoe bats 1972-2012. The relationship is not statistically significant.
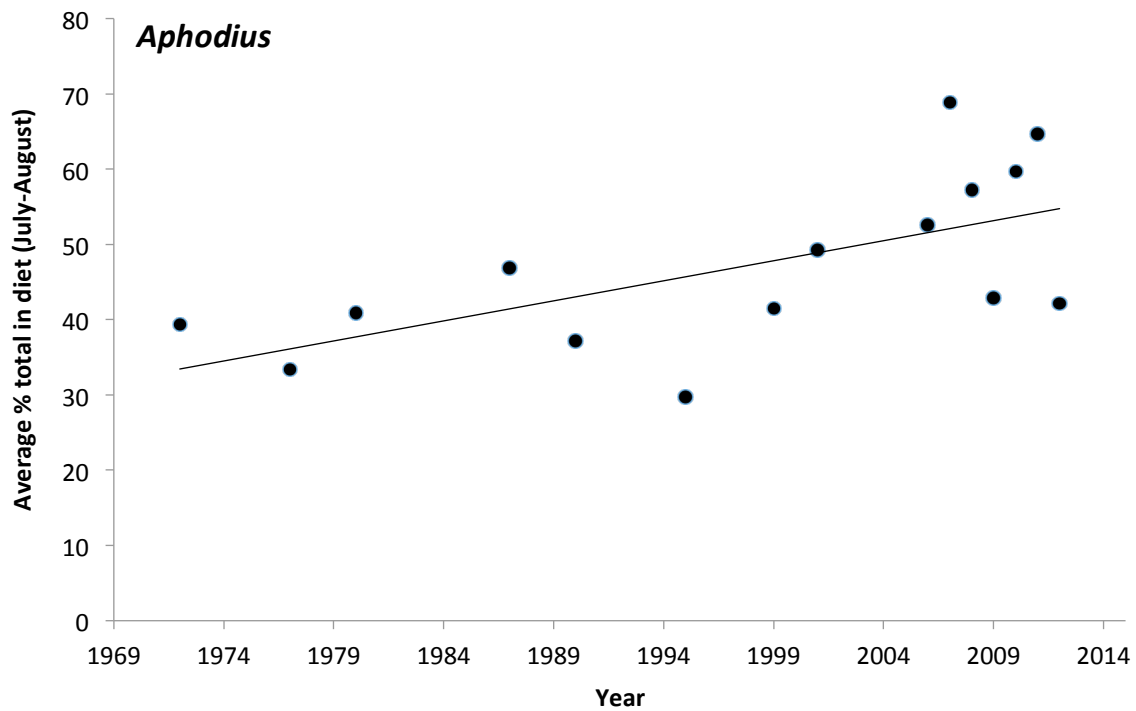
Figure 11. Changes in the abundance of *Aphodius* spp. in the diets of Woodchester greater horseshoe bats 1972-2012. The positive correlation is statistically significant ($r_{s\ 15} = 0.68$, $P < 0.01$).
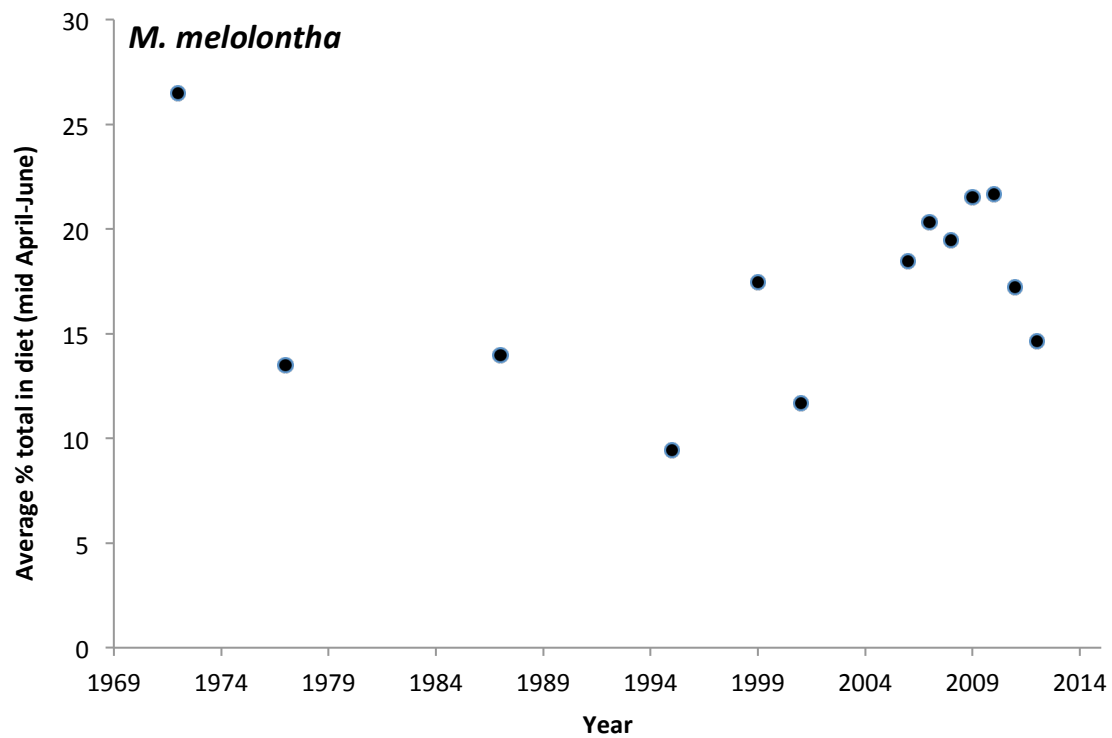

Figure 12. Changes in the abundance of cockchafers (*M. melolontha*) in the diets of Woodchester greater horseshoe bats 1972-2012. The relationship is not statistically significant.

Discussion

Diet phenology

Mean birth dates of bats at Woodchester Mansion have been getting earlier since the late 1960's and this may be linked to our findings that spring appearances of key prey items are also shifting forwards (*M. melolontha* and Tipulidae). Birth date in greater horseshoe bats is affected by spring climate in the south-west of Britain, with warmer April/May temperatures being a predictor of early births at three sites, including Woodchester Mansion (1984-1993) (Ransome & McOwat, 1994). A late birth date in 1986 at these sites also preceded subsequent colony declines. Therefore climate change since the 1960's may have contributed to the overall trend towards earlier key prey emergence and earlier births in bats at Woodchester. Number of births and colony counts are also generally on the increase at this site, which may also be an indirect consequence of a series of warmer springs. Numbers of births also appear to be positively related to abundance of *M. melolontha* in the bats' diets (1972-2009), which seems to be increasing although sample sizes were too small to analyse this statistically.

Golden plovers (*Pluvialis apricarial*) and their tipulid prey are also probably affected by climate change (Pearce-Higgins *et al.*, 2005). First-laying dates were earlier in golden plovers when warmer April and May temperatures were recorded and their tipulid prey also emerged later with warmer May temperatures. The authors warn that projections under climate change scenarios over time may suggest a mismatch between tipulid prey emergence and egg-laying dates of this birth species, which could reduce breeding success in the long run.

M. melolontha, being a single species and a high quality first choice prey item for greater horseshoe bats (Jones, 1990; Ransome 1996; 1997; 2000), is a useful model to explore how diet phenology is linked to climate. Timing of *M. melolontha* swarming can also be predicted by spring air temperatures (Wagenhoff *et al.,* 2014). Warmer springs may therefore be contributing to the earlier peak appearance of this key prey item in diets of bats at Woodchester Mansion. Plasticity in birth timing in the short term may therefore have positive implications for greater horseshoe bat conservation, as timing foetal development earlier may allow mothers to benefit from spring peaks of high quality prey.

The phenology of crane flies (Tipulidae) is more difficult to interpret as the family contains a number of species, which may account for the defined peaks in the bats diets in spring and autumn (Figures 7, 8). We would expect that spring peaks in tipulids are positively related to date of birth of bats, as they are an important food source early in the year when other preferred prey groups such as moths or *M. melolontha* are scarce (Jones, 1990; Ransome, 1996; 1997; 2000). Autumn peaks in tipulids would not affect birth timings, being after the event. Insect DNA extracted from faecal samples of greater horseshoe bats collected at ten maternity roost sites in south-west Britain (including Woodchester Mansion) revealed at least six species of tipulids (including *Tipula fascipennis, T. fulvipennis, T. lunata, T. paludosa, T. scripta* and *T. subcuntans*) (Rasmussen, 2014). Of the species identified, *T. fascipennis* and *T. lunata* could account for the spring peak in the bats' diets and *T. fulvipennis* and *T. paludosa* could account for the autumn peak (based on when adults are flying: Nature Spot,

2014). Emergence of *T. fascipennis* and *T. lunata* could therefore be dependent on spring temperatures, similar to the tipulid prey of the golden plover and therefore be affected by climate change over time (e.g. Pearce-Higgins *et al.*, 2005). However other factors such as rainfall and winter temperatures may also affect overall prey abundance in spring and summer, which in turn could impact breeding success of greater horseshoe bat colonies, as in the case with European starlings in British Columbia (Williams *et al.*, 2015). Development of the starling's tipulid prey is thought to be affected by winter temperatures, which can predict breeding phenology of the species (Williams *et al.*, 2015). This is important as it is not just timings of emergence of key prey that may affect greater horseshoe bat colonies but also abundance of insects at these key times.

Implications of possible changes in prey abundance

Moths and small dung beetles (*Aphodius*) are also important prey groups for greater horseshoe bats in Britain (Jones, 1990; Ransome, 1996; 2000). However moths appear to be declining in bats' diets (at least since 1995) at Woodchester Mansion and *Aphodius* are increasing. Significant declines in moths (40% in the south of Britain since 1968) may explain the decrease in abundance of this group in the diet of bats at Woodchester Mansion since the 1980's (Fox *et al.*, 2013). For example, the heart and dart (*Agrotis exclamationis*), a moth species considered to be eaten often by greater horseshoe bats (Ransome, 1996), has declined over 70% since 1968 and the dark arches moth (*Apamea monoglypha*), another key prey species, is also declining (Conrad *et al.*, 2006; Fox *et al.*, 2013). However another key species eaten by greater horseshoe bats, the large yellow underwing (*Noctua pronuba*) has increased in numbers by over 100% and the small yellow underwing (*N. comes*) is also on the increase (Conrad *et al.*, 2006; Fox *et al.*, 2013). Generally, as southern moth populations are decreasing, there has also most likely been a decrease in diversity. As our moth identification in faecal samples is only to order, individual species declines cannot be observed. It would therefore be interesting to analyse changes in moth species diversity over time in the same sub-samples used in this project, using genetic techniques, and this is currently being completed. Scottish farms that had implemented agri-environment schemes had a higher abundance of moths than those that were not involved in the schemes (Fuentes-Montemayor *et al.*, 2011). Therefore the continued implementation of such schemes around maternity roosts may have a positive effect over time, increasing moth abundance in diets in the future. To determine if such schemes are increasing key greater horseshoe prey species, future work could involve insect trapping and bat activity surveys in areas around maternity colonies that are or are not involved in stewardship schemes.

The positive increase in the incorporation of *Aphodius* in the diet since the late 1960's may be due, in part to the decrease in Lepidoptera available in the diet. Greater horseshoe bats are highly selective in their prey choice (e.g. Jones, 1990; Ransome 1996; 1997) and with a declining availability of moths, the bats may be focusing on the next best available prey, *Aphodius*. The increase in *Aphodius* in bats' diets over time may also be linked to implementation of habitat management specifically targeted at increasing cattle and therefore key prey species (including *Aphodius*) in the area surrounding the maternity roost at Woodchester Mansion (e.g. Ransome, 1996; 2000; Duvergé & Jones 2003; Longley, 2003). *Aphodius* beetles are important prey for juvenile greater horseshoe bats, who are generally

on the wing and able to exploit peak populations of this night flying beetle by mid-summer (Ransome, 1996). It is also an important prey species for adult bats (especially lactating females), when preferred prey such as moths are scarce (Ransome, 1996). Availability of this beetle is therefore an important factor in colony survival. For example, the outbreak of foot and mouth disease and associated slaughter of grazing livestock in the Forest of Dean in Gloucestershire in 2001 meant a fall in local *Aphodius* populations, which in turn affected greater horseshoe bat colonies in the area (Ransome & Priddis, 2005). Juveniles in the local colony and even those at Woodchester Mansion, where there was no local slaughter, were of worse body condition and survival rates were low (Ransome & Priddis, 2005). Therefore habitat management under stewardship schemes, that aimed to increase local *Aphodius* populations should, in theory be in part responsible for the increase in *Aphodius* seen in greater horseshoe bats' diets at Woodchester Mansion. Again as with the moths, this would need to be investigated further before we can be confident that the trends observed are not due to other factors. The genus *Aphodius* also comprises a number of species, and it is not certain which species are most represented in this study. However it is likely that the vast majority are *A. rufipes*, a large species and also one that is nocturnal (Landin, 1961), so likely to be profitable over smaller nocturnal species and the larger diurnal *A. fossor* (Ransome, 1996). Identification of scarab beetles is difficult when more than one species with similar morphological features are present and therefore it is also likely that there is some misidentification of *Amphimallon* spp. as *Aphodius* spp. in mid-summer samples (before first week in July). These June samples were not used in the analysis, so will not have affected the results.

Implications for greater horseshoe bats

Analysing changes in the phenology of key prey in the diets of greater horseshoe bats in relation to timing of birth has provided insight into how changes in climate may be affecting both phenomena. This is important for greater horseshoe bat conservation in Britain, as plasticity in birth timing is likely to be advantageous if the appearance and abundance of key prey species is changing. Whether plasticity in birth timing is heritable, and therefore subject to natural selection, is currently being analysed (Ward, Ransome, Jones, Wilson & Rossiter, *in prep.*). However, further analysis and predictions of likely long term effects of climate change on birth timings and prey emergence are important to investigate, as in future, mismatching of birth and prey emergence timings may be ultimately disadvantageous for the species (e.g. Pearce-Higgins *et al.*, 2005).

Results from this project could also be compared to those from molecular analyses of sub-samples collected over the same time period, due to be performed by Kristine Bohmann at the University of Copenhagen. Molecular analysis will yield different information from what has been found in this study and so will hopefully complement our findings, for example perhaps giving a more detailed picture of changes at a species level. Comparison of changes in diversity of moth species in diet since the 1960's over time would be an interesting avenue to explore for example. Future work will also include investigation of the impact of habitat management under stewardship on insect abundance and diversity, as well as colony growth and foraging activity of greater horseshoe bats. This work will be carried out as a PhD by Jérémy Froidevaux 2015-2018.

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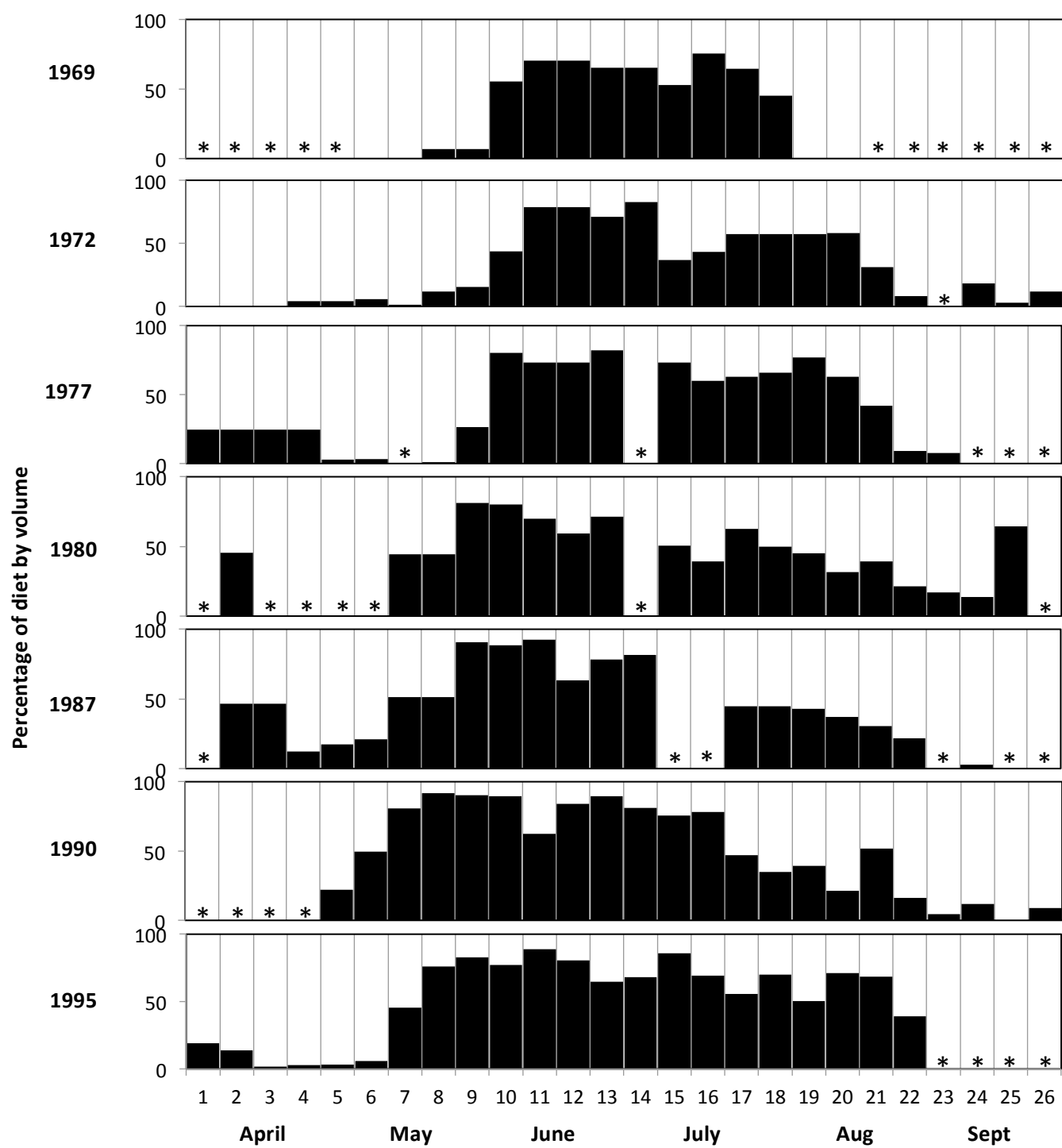
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Appendix: Phenological changes in key prey items in the diet (mean % volume) of greater horseshoe bats at Woodchester 1999-2012. Missing data indicated by *.
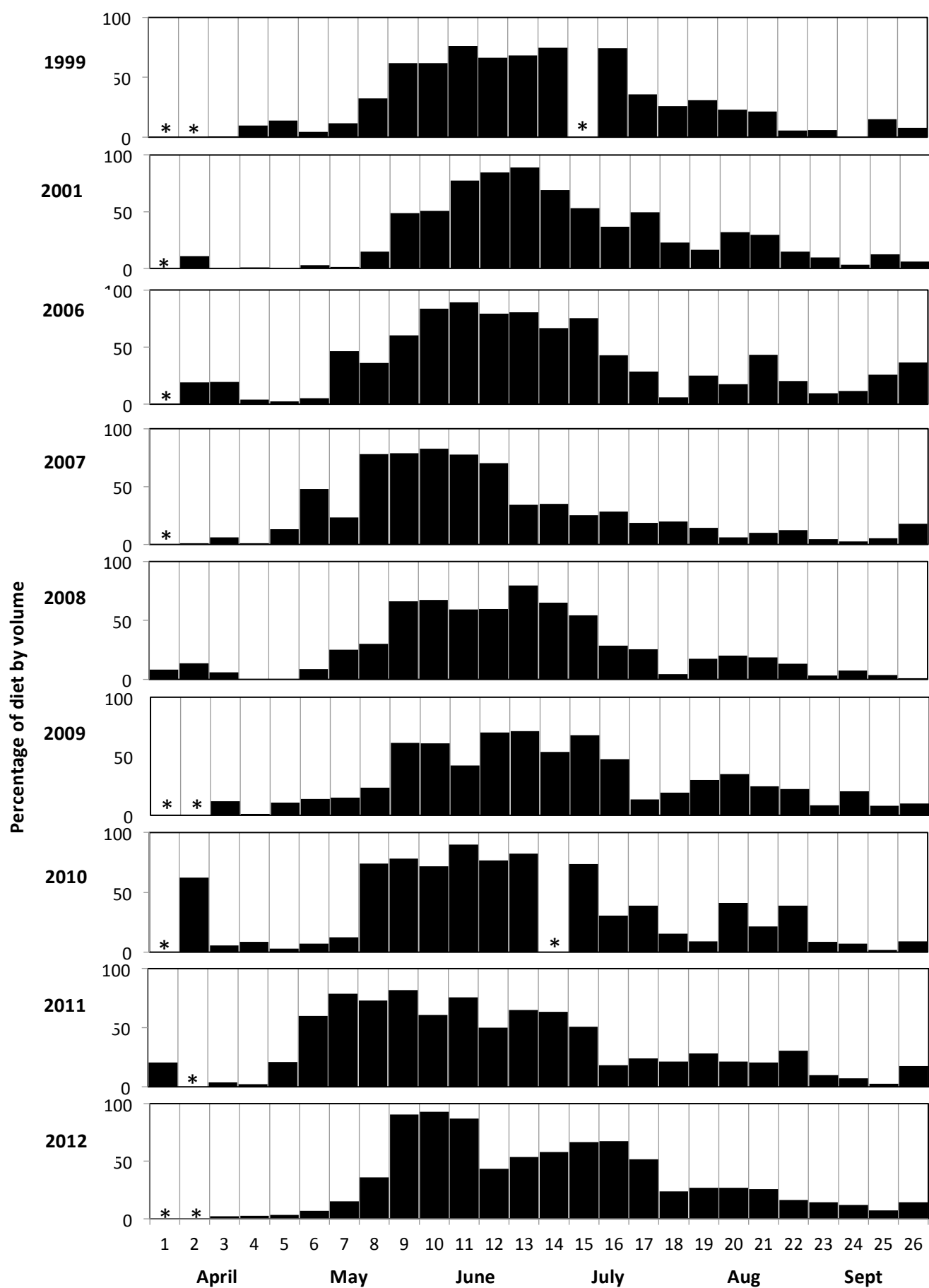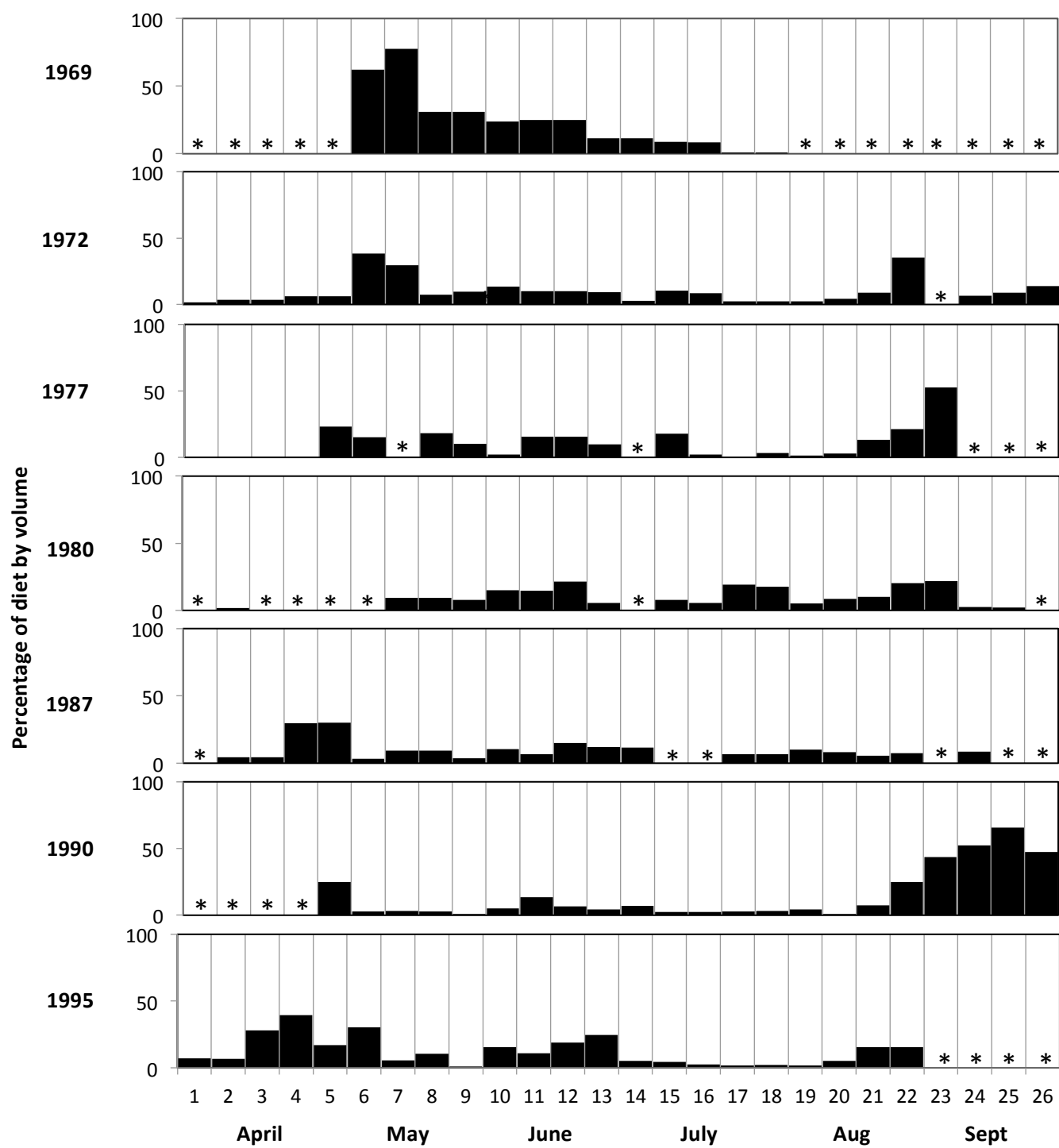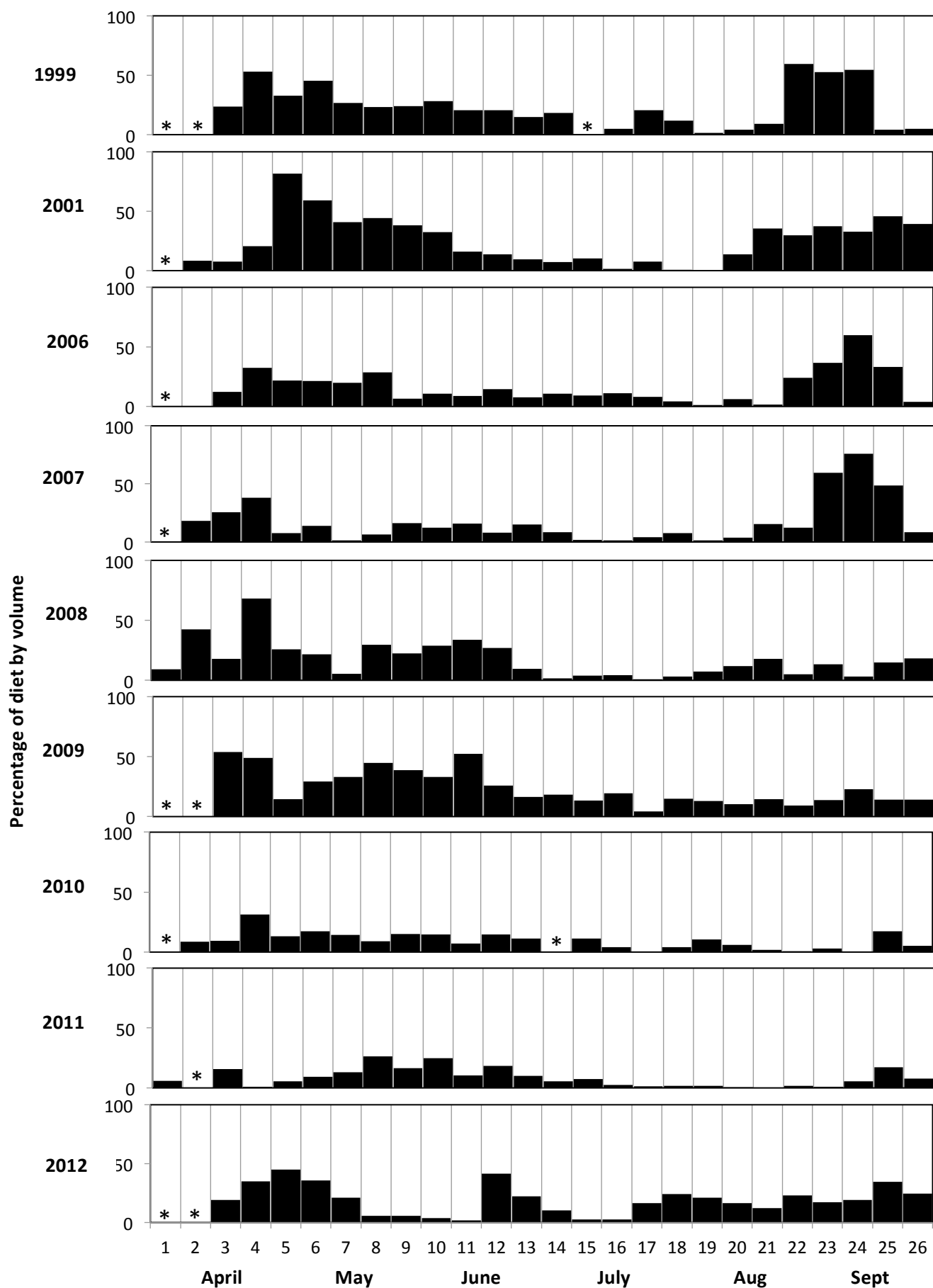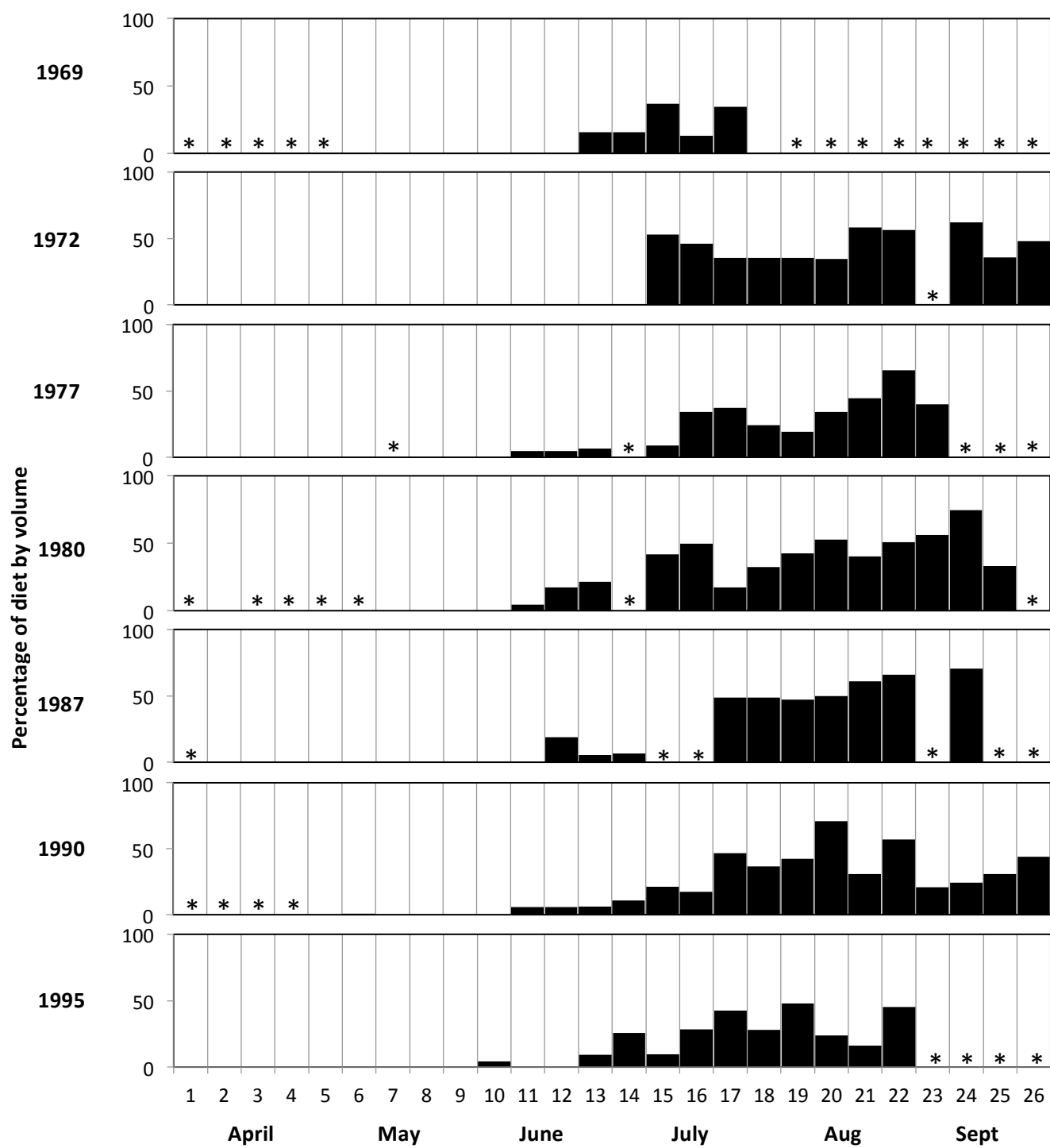
M. melolontha

M. melontha

Percentage of diet by volume
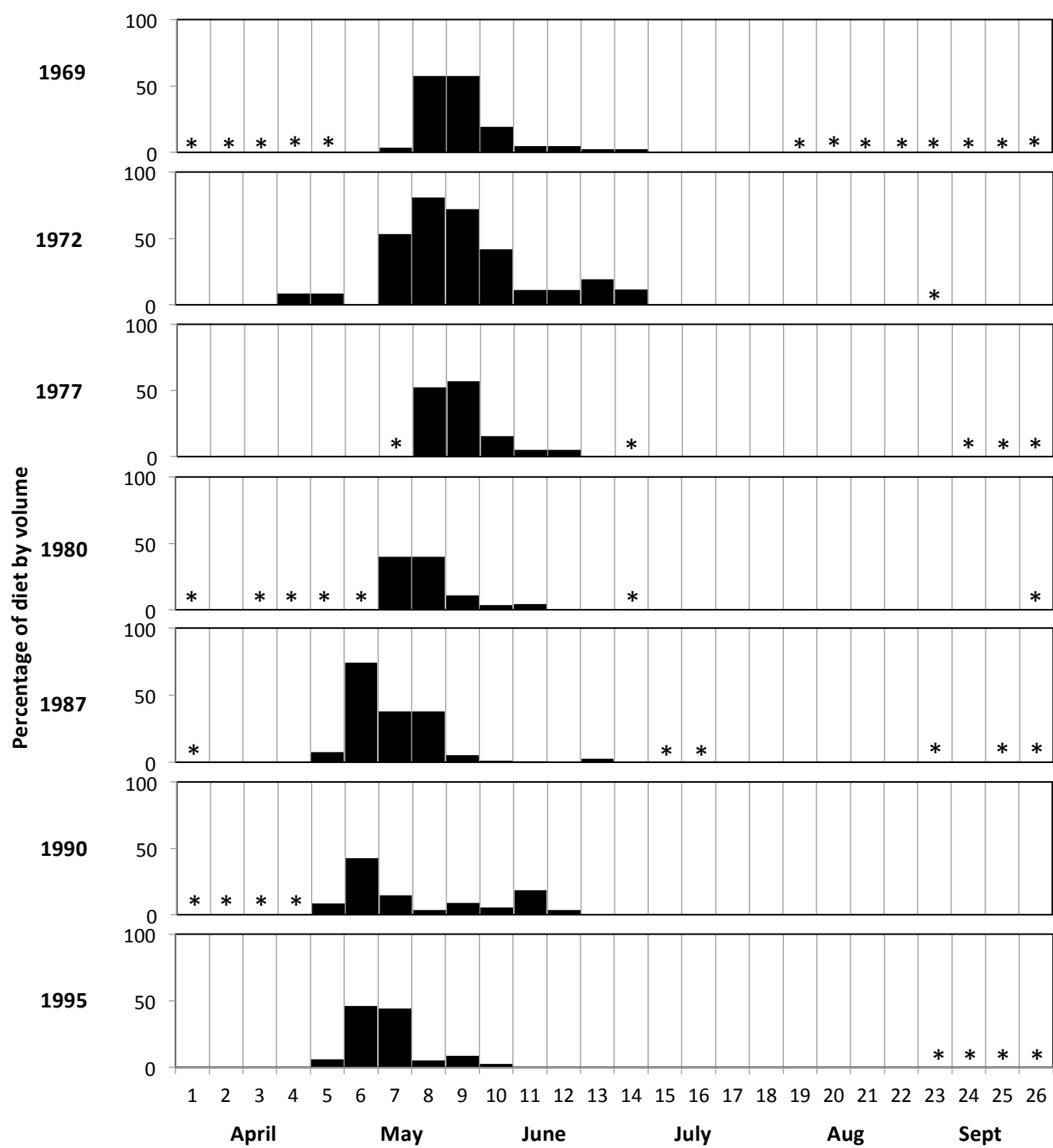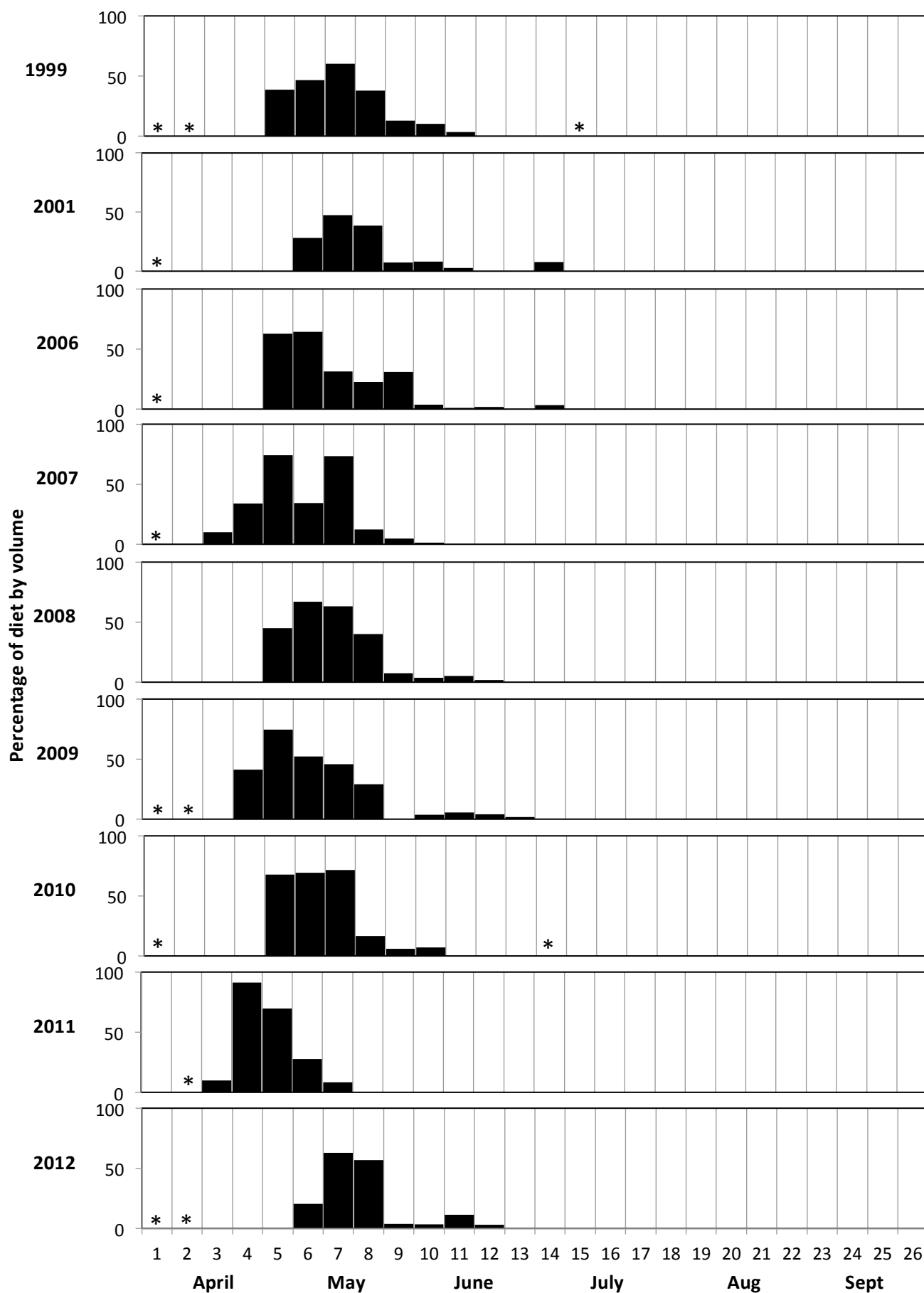
Lepidoptera

Lepidoptera

Percentage of diet by volume

1999, 2001, 2006, 2007, 2008, 2009, 2010, 2011, 2012

April   May   June   July   Aug   Sept

Tipulidae

Percentage of diet by volume, plotted for the years 1969, 1972, 1977, 1980, 1987, 1990, and 1995 across periods 1–26 from April through September.

Tipulidae

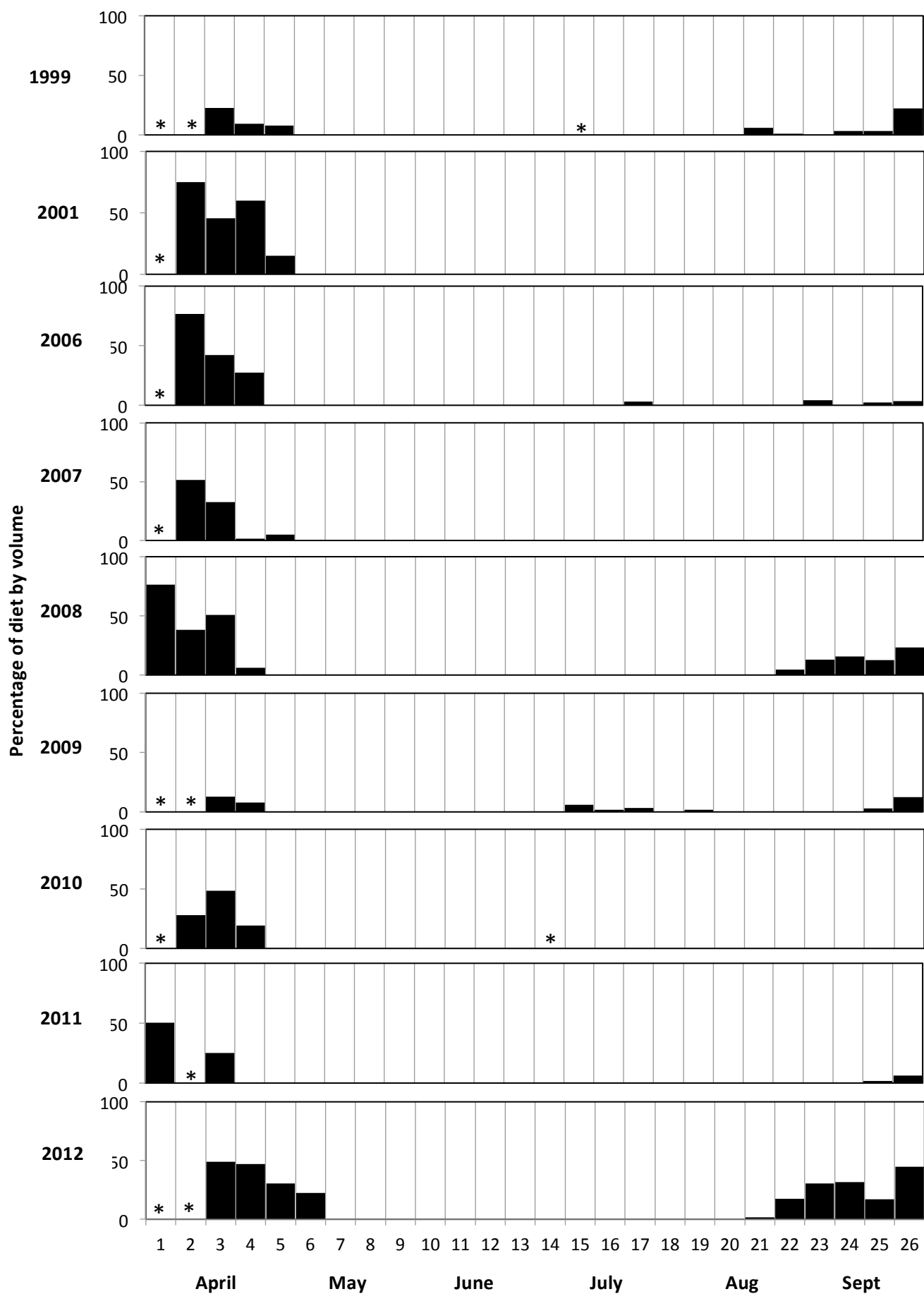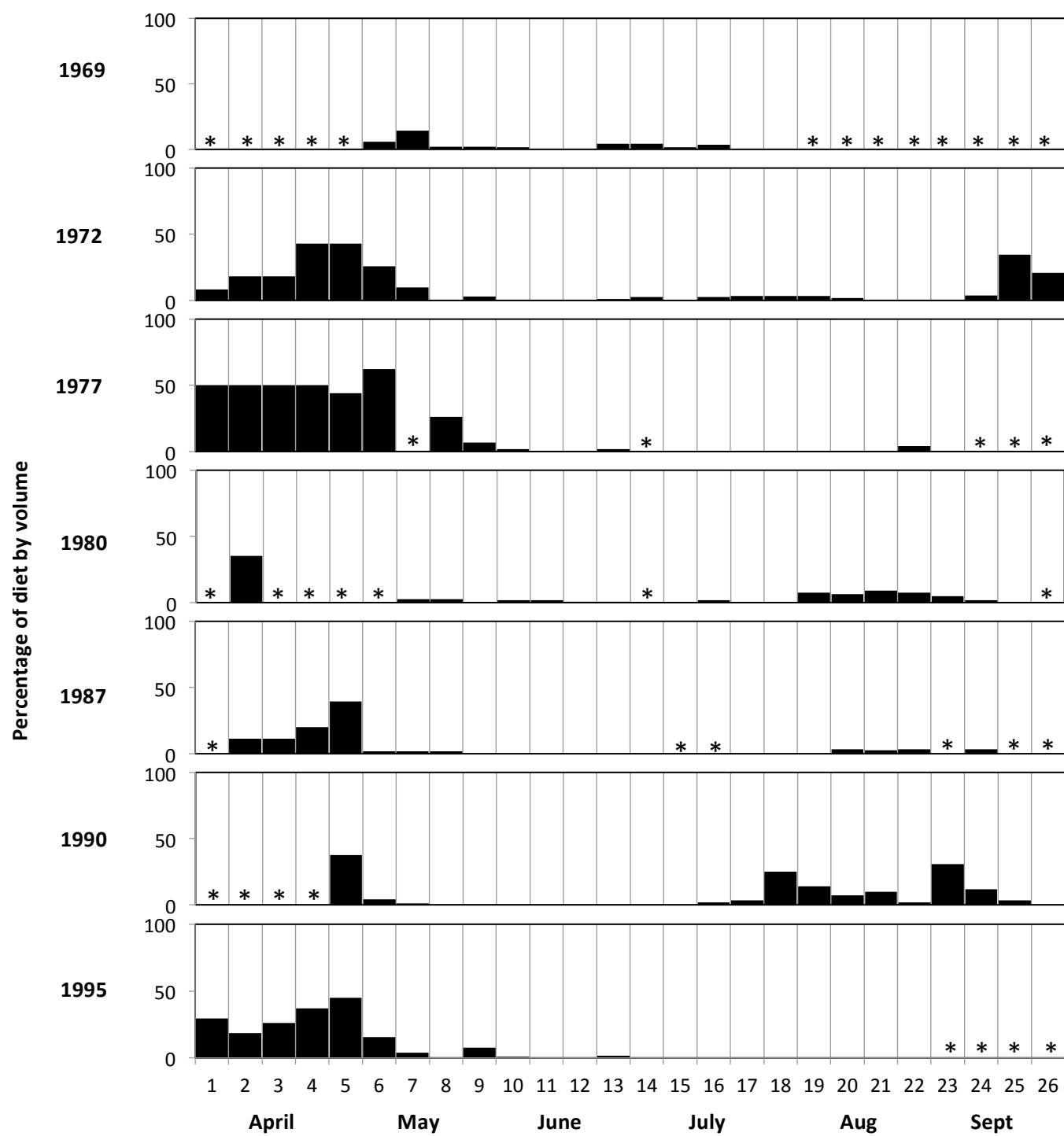*Aphodius* spp.

Aphodius spp.
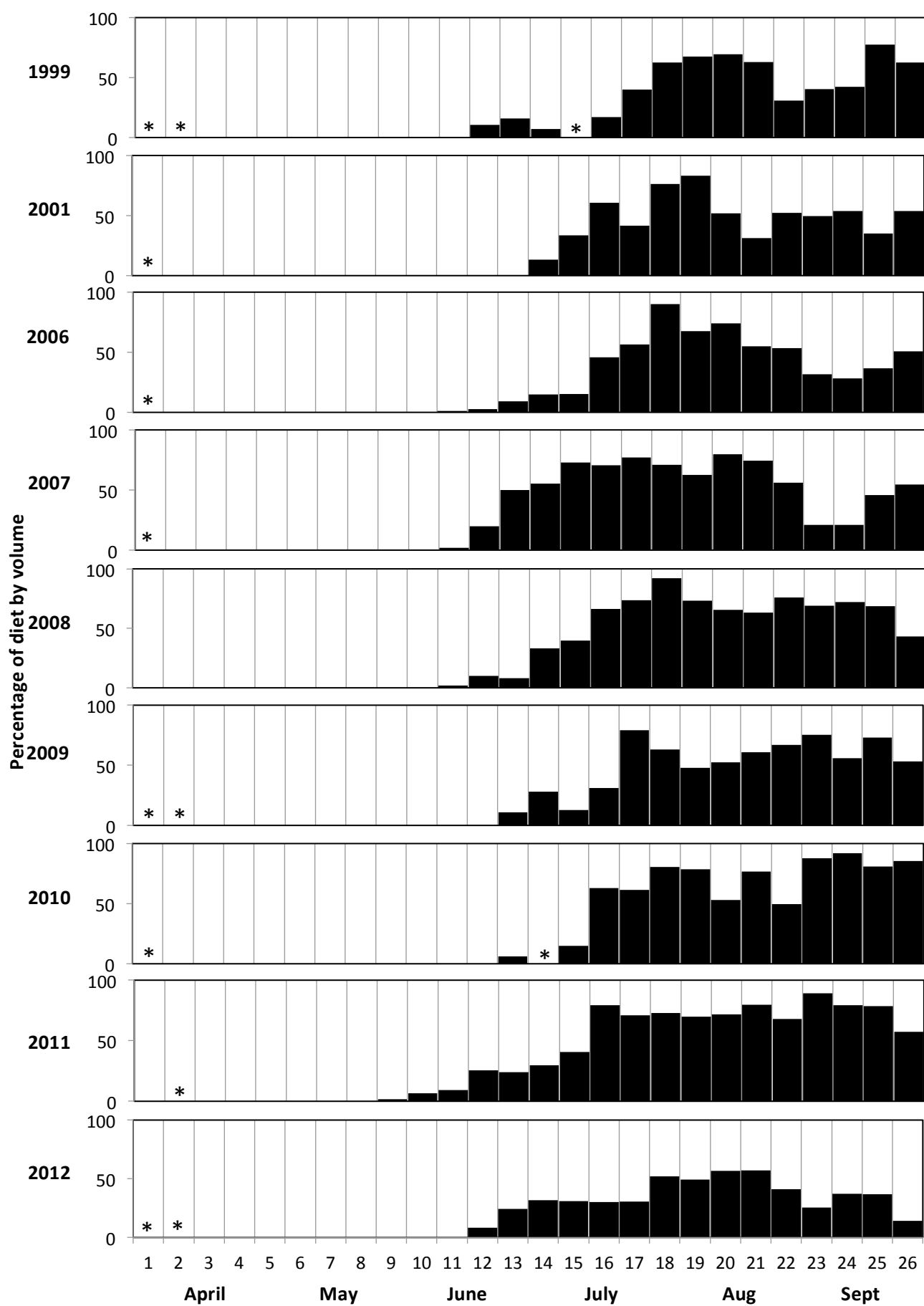
Geotrupes spp.
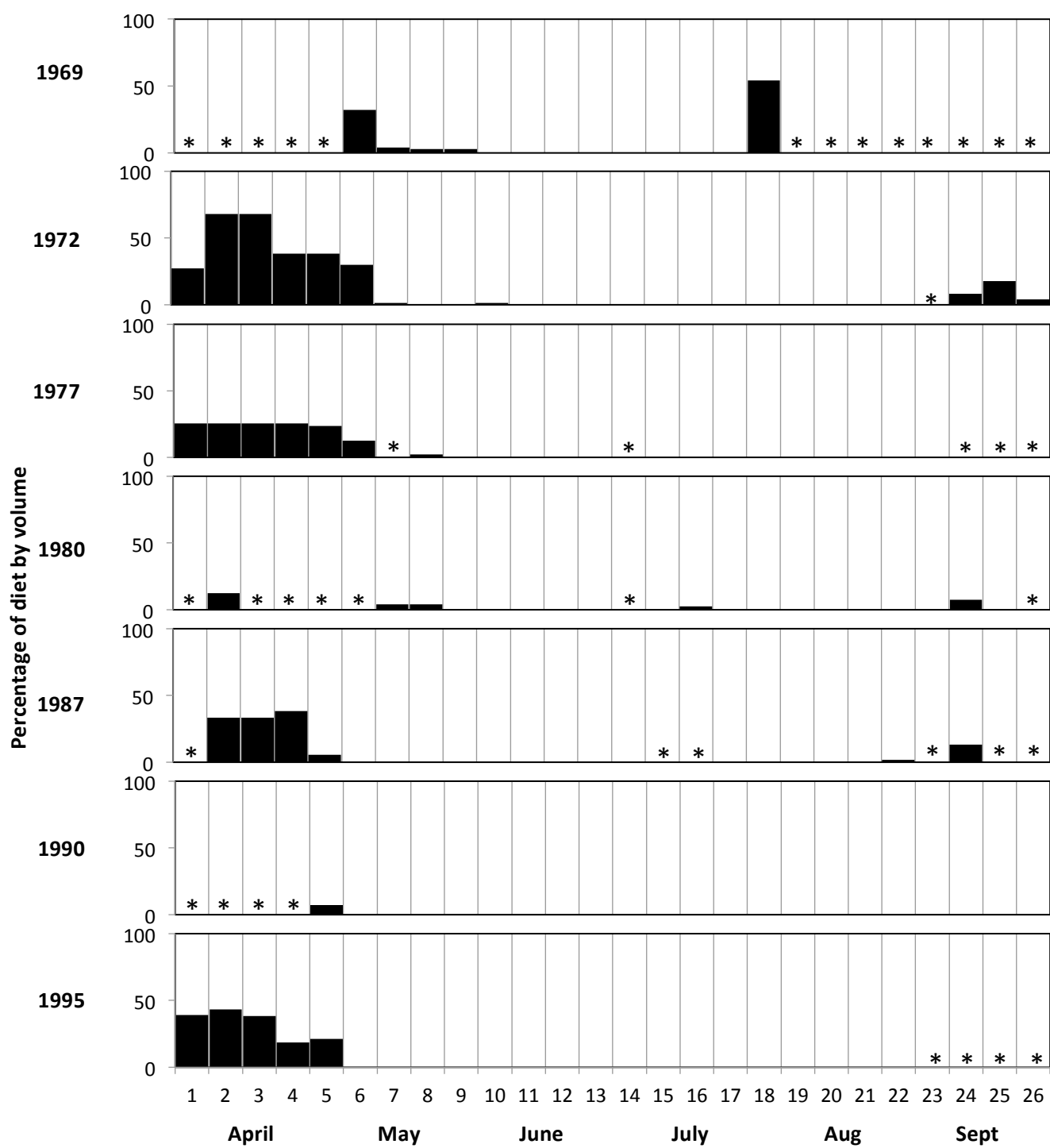
Geotrupes spp.

Ichneumonidae

Ichneumonidae