THE ROLE OF INVERTEBRATES IN THE DIET, GROWTH AND SURVIVAL OF NORTHERN BOBWHITE, *COLINUS VIRGINIANUS*, CHICKS IN THE SOUTHEASTERN UNITED STATES.

DAVID ANTHONY BUTLER

A thesis submitted in partial fulfilment of the requirements of
Liverpool John Moores University for the degree of Doctor of
Philosophy

This research programme was carried out in collaboration with the
University of Georgia and Tall Timbers Research Station, USA,
and The Game Conservancy Trust, UK

July 2007

ABSTRACT

The role of invertebrates in the diet, growth and survival of northern bobwhite, *Colinus virginianus,* chicks in the southeastern United States.

Invertebrates are the primary component in the diet of northern bobwhite, *Colinus virginianus*, chicks during the first two weeks of life. Despite this, few studies have described the composition of invertebrates in the diet of wild chicks and none have examined their effects on chick-growth and survival. Here, a three-year study was conducted to examine the role of invertebrates in the diet of northern bobwhite chicks in the southeastern United States.

Initially, laboratory feeding-trials were conducted to evaluate the use of faecal analysis for studying the invertebrate diet of northern bobwhite chicks. Then, by accounting for differential recovery of prey items, the invertebrate diet of bobwhite broods on farmland and forested plantations in Florida and Georgia was determined by analysing faeces collected from their nocturnal roost sites. These broods were also captured at 10-days old to provide data on chick-growth and survival. Invertebrate-selection by bobwhite chicks was studied by comparing the composition of invertebrates in the diet of chicks to that found in brood-rearing habitats. In addition, the invertebrate-selection of human-imprinted chicks in the same habitats was also examined and compared to that of the wild chicks. Finally, because cotton is a major crop in the southeastern United States, a field-scale study was conducted to examine how crop-management differences between insect resistant and non-insect resistant cotton varieties affect the abundance of bobwhite chick-food invertebrates.

Invertebrate selection by both wild and human-imprinted chicks was non-random. Although invertebrate composition in the diet of chicks differed between all sites, the three invertebrate groups most selected by wild bobwhite chicks, Hemiptera, Coleoptera and Hymenoptera, collectively formed over 70% of the invertebrate-diet on all study sites. Although invertebrate-composition in the diet had no effect on chick survival, growth rates of chicks were lower in those broods that had a high proportion of the least selected prey items in their diet. The invertebrate selection of human-imprinted chicks was similar to that of wild chicks, suggesting that invertebrate selection by bobwhite chicks is innate. In the cotton study, half-fields planted to an insect resistant cotton variety received fewer applications of insecticide than those planted to a non-resistant variety. Consequently, a greater abundance of bobwhite chick-prey invertebrates were found in the insect resistant cotton crops.

This study has identified those invertebrate groups most important in the diet of wild northern bobwhite chicks. Management prescriptions can now be designed and developed to specifically increase the abundance of these prey items within brood-rearing habitats.

Dedication

To my Parents

Thank you.

ACKNOWLEDGEMENTS

Firstly, I wish to thank my family, especially my wife Fiona. Their tireless support has made pursuing my chosen career and interests possible.

I would especially like to thank my supervisors, Simon Dowell and Mark Feltham at Liverpool John Moores University and Bill Palmer at Tall Timbers Research Station, for all their advice and support during my PhD. I also received much help from John Carroll at the University of Georgia and Rufus Sage, Nick Sotherton and Nicholas Aebischer from The Game Conservancy Trust. I also thank Steve Moreby from The Game Conservancy Trust for his patience and invaluable assistance while I learnt the fine art of identifying insects from the tiniest fragments of shell and other body parts!

At Tall Timbers, I have many people to thank for their help and hospitality. Firstly, all the technicians and interns of the gamebird lab between 2002 and 2005: Travis Anderson, Mike Blondin, Fiona Campbell, Katherine Crook, Tina Hannon, Mike Juhan, Vanessa Longsden, James Martin, Rob Olson, Shane Roethle, Matt Stover, Ryan Tipton and Brent Widener. Any help that you gave during my PhD was much appreciated. I am especially grateful for all the advice and help I received from Shane Wellendorf. Shane, I apologize again for the clay and 'wing-dinger' incident! Outside of the gamebird lab, Lisa Bagget, Kaye Gainey, Jerome Golden, Kathy Marois, Joe Noble and Eric Staller provided invaluable assistance with various things, including sorting bugs, administration, computers and housing chicks. It was an honour meeting and working with you all.

Without the many farmers in Laurens county, Georgia, kindly allowing access to their properties, the study of bobwhite broods on farmland would not have been possible. I would particularly like to thank James Wood and Mike Hogan who very kindly allowed me to conduct the cotton project on their farms. Thanks to Patrick Cook for his help, southern comedy and unique way of looking at life. Cheers mate!

Funding for this project was provided by Monsanto, The University of Georgia, Tall Timbers Research Station and The Game Conservancy Trust. This research was approved by the Tall Timbers Research Station Institutional Animal Care and Use Committee on August 21st 2001 under protocol GB-2001-01.

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INTRODUCTION TO THESIS

1.0 INTRODUCTION

1.1 Status of the northern bobwhite

While the northern bobwhite, *Colinus virginianus*, (henceforth, bobwhite) remains the most widely distributed and abundant quail species in the United States, it has declined rapidly during the last 50 years (Figure 1.1). Analysis of data from the North American Breeding Bird Survey (BBS) (Church *et al.* 1993, Burger 2001) and the Christmas Bird Count (CBC) (Brennan 1991) show significant bobwhite population declines in the majority of states within its geographic range. Declines have been particularly marked in southeastern states with, for example, populations declining in Florida and Georgia at rates of 3.4% and 4.3% per year respectively between 1966 and 1999 (Burger 2001). Despite concomitant falls in harvest rates, the bobwhite remains an economically important gamebird in this region (Burger *et al.* 1999).

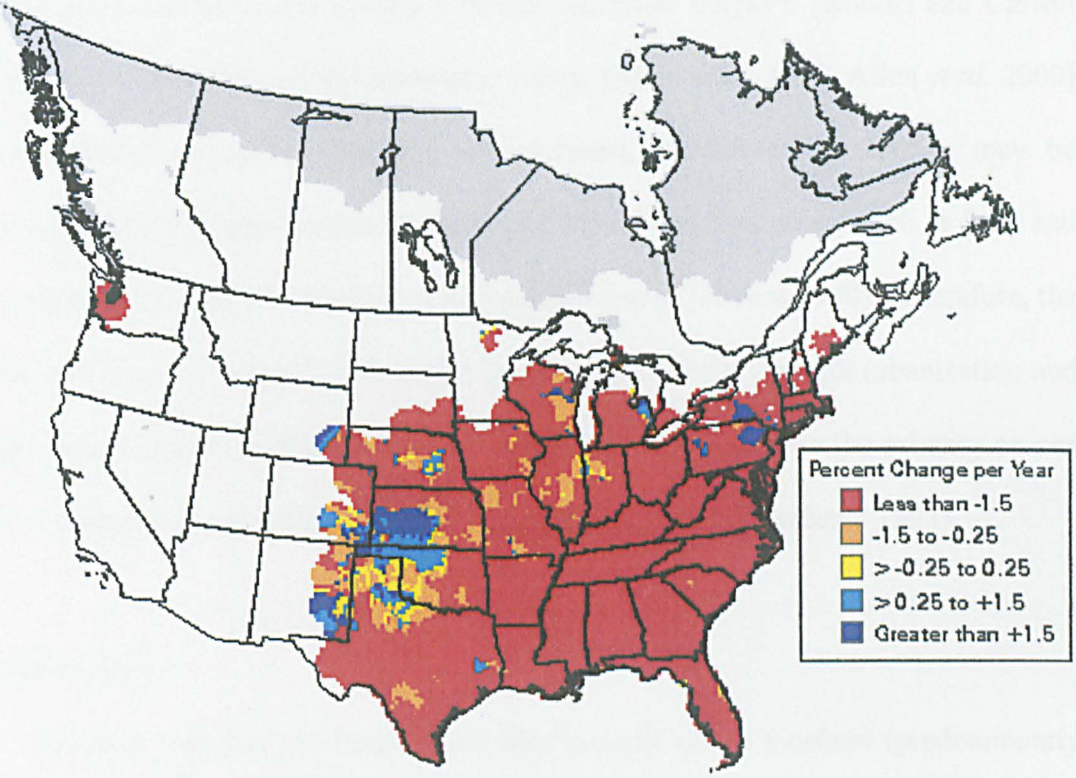

Figure 1.1. Distribution and population trends of northern bobwhite in North America, 1966-2003. Data taken from the North American Breeding Bird Survey (Sauer *et al.* 2005).

1.2 Causes of decline

Whilst studies have suggested that pressure from predators, both native (e.g. raccoons, *Procyon lotor,* and Cooper's hawks, *Accipiter cooperii* [Rollins and Carroll 2001]) and non-native (fire ants, *Solenopis invicta,* [Allen *et al.* 1995, Allen *et al.* 2000] and nine-banded armadillo, *Dasypus novemcinctus*, [Staller *et al.* 2005]), may be suppressing bobwhite populations, at least on a local level, resources, such as food and cover, provide the ultimate check on bird population size (Newton 1998). Therefore, the regional reduction in quantity and quality of bobwhite habitat through urbanization and changes in agricultural and silvicultural practices are believed to be the primary causes of the widespread decline (Brennan 1991, Church *et al.* 1993, Roseberry 1993).

1.2.1 Silviculture

In many southeastern states, much land once in native pineland (predominantly longleaf pine, *Pinus palustris*), agriculture or marginal habitats has been replaced by commercial timber stands (Brennan 1991, Kautz 1998). The silvicultural practices employed in these areas are not conducive to creating bobwhite habitat. The uniform spacing and high stocking density of the trees creates a closed-canopy 2-5 five years post planting that eliminates grasses and herbaceous plants that are important for food, shelter and nesting (Brennan 1991). Furthermore, in many of the remaining areas of native pineland, changes in management have devalued these areas for bobwhite. The controlled burning of patches of forest in spring and early summer is no longer a commonly used management tool (Brennan 1991) (Plate 1.1).

Plate 1.1. Prescribed burns on 1-2 year rotations prevent the build up of leaf litter and encourage the growth of weedy vegetation.

Burning on short rotations of 1-2 years creates a patchwork of areas for nesting, cover and foraging (Stoddard 1931). By burning vegetation during spring and early summer the availability of invertebrates to bobwhite chicks in these areas can be increased markedly by encouraging the growth of weedy vegetation (Hurst 1972). In addition, annually disking firebreak-lanes also stimulates the growth of plants that host invertebrates during the summer and provide seeds through the autumn and winter (Stoddard 1931).

The intensive management of forest habitats for bobwhite does, however, still occur on the privately owned bobwhite hunting plantations in the Red Hills region in southern Georgia and northern Florida. Management operations, including controlled burning, supplemental feeding and predator control, aim to provide surplus stocks of wild bobwhite for shooting. However, the high cost associated with these management techniques coupled with the time lag between their implementation and an adequate stock of birds for shooting, has probably made the release of pen-raised birds an increasingly attractive option (Kozicky 1993, DeVos and Speake 1995). Paradoxically, this 'quick fix' method for increasing stocks may have contributed to the decline of wild bobwhite through the introduction of disease, competition for resources or attracting predators (Davidson *et al.* 1982, Brennan 1991, Robison and Brennan 1992).

1.2.2 Agriculture

Agricultural intensification over the last half century has been cited as a major contributory factor in causing the decline of bobwhite and other farmland bird species in North America (Vance 1976, Church *et al.* 1993, Blackwell and Dolbeer 2001, Murphy 2003). Although various aspects of modern farming have contributed to the decline of bobwhite in agricultural landscapes, those most often cited are a loss of marginal habitats and an increase in pesticide use (Brennan 1991, Burger 2001). As a consequence of increasing farm and field-size to accommodate modern machinery and production systems, there has been a loss of marginal habitats that are important areas for nesting, brood-rearing and over-wintering (Exum *et al.* 1982, Taylor *et al.* 1999, Cook 2004). In 1940, the average farm size in the United States was 39 hectares; by 1997 this had nearly tripled to 108 hectares (www.nass.usda.gov).

An integral component of agricultural intensification has been the development and use of pesticides. The dramatic increase in the use of herbicides and insecticides since the Second World War (Donaldson *et al.* 2002) has lead to clean-farming practices where insect and weed populations are much suppressed in cropped fields (Wilson *et al.*

1999). In addition to reducing the abundance of seeds for adult gamebirds during winter and spring (Draycott 2002), the destruction of weeds in cropped fields diminishes the number of invertebrates available to chicks during the summer (Rands 1985, Moreby and Southway 1999). Reducing the abundance of important gamebird chick-prey invertebrates in cropped fields either by direct kill (insecticides) or through the removal of host plants that support phytophagous species (herbicides) has been shown to reduce grey partridge, *Perdix perdix*, chick survival (Potts 1986). Although these links have not been clearly demonstrated with bobwhite, they are strongly suspected (Stromborg 1982, Brennan 1991). Bird mortality from direct exposure to pesticides is rare, although some sub-clinical effects have been reported (Stromborg 1982, Somers *et al.* 1991, Palmer 1995).

Some biologists are concerned that agriculture has been further intensified through the introduction of Genetically Modified (GM) crops (Watkinson *et al.* 2000, Krapu *et al.* 2004). Since their introduction in 1995, farmers in the United States have rapidly integrated them into the farming system. For example, GM cotton, *Gossypium spp.*, varieties accounted for 73% of the total cotton area planted nationally in 2003 (Economic Research Service/United States Department of Agriculture (ERS/USDA), http://www.ers.usda.gov). Although, in comparison to conventional crops, little research has been conducted into the direct and indirect effects of GM crops on invertebrate and weed populations, a farm scale study carried out in Great Britain suggests that their response is dependent on crop type (Haughton *et al.* 2003, Heard *et al.* 2003). As no studies have specifically examined the abundance of gamebird chick-invertebrate prey in GM crops, the foraging value of these widely grown crops in the United States is unknown.

1.3 Chick diet

1.3.1 Importance of invertebrates

The diet of bobwhite and other gamebird chicks consists primarily of invertebrates during the first two weeks of life (Stoddard 1931, Green 1984, Hill 1985). Despite this, few published studies that have described the invertebrate diet of wild bobwhite chicks (Stoddard 1931, Hurst 1972). In both of these small studies, the description of the stomach contents of captured chicks lacked detail, with invertebrates only being classified to order. Furthermore, because neither of these studies related invertebrate composition in the diet to abundance in brood-rearing areas, the relative selection for different prey items is unknown.

Surprisingly, given that chick survival is recognized as one of the most important aspects of the bobwhites' biology (Roseberry and Klimstra 1984), the importance of invertebrates in the diet has only ever been examined in captive-reared chicks (Palmer 1995). In a laboratory feeding study, the growth rates of bobwhite chicks fed a diet containing few invertebrates were lower than those fed an invertebrate-rich diet (Palmer 1995). Palmer (1995) concluded that a 7-10 day old bobwhite chick requires approximately 6g of invertebrates daily to maintain normal growth rates. In grey partridge chicks, an invertebrate-poor diet has also been shown to reduce feather development and survival (Liukkonen-Anttila *et al.* 2002, Southwood and Cross 2002). In field studies, the composition of the invertebrate diet of grey partridge and ring-necked pheasant, *Phasianus colchicus,* chicks has been related to chick survival (Green 1984, Hill 1984). In both species, chick survival to 21 days was related to the proportion of preferred invertebrates in their faeces.

1.3.2 Measuring prey-supply

Due to the importance of invertebrates, researchers often index the foraging value of bobwhite brood-rearing habitats according to the relative abundance or biomass of invertebrates (Burger *et al.* 1993, DeVos and Mueller 1993). However, measuring abundance using standard entomological techniques, such as sweep-netting, suction samplers and pit fall traps, does not incorporate a measure of availability or selection. By not accounting for these factors, biologists may misjudge the true foraging value of habitats because not all invertebrates present will be available to or selected by chicks. To provide a more biologically relevant assessment of bobwhite chick food-supply, researchers have begun examining the diet of captive-reared chicks allowed to forage in different brood-rearing habitats (Hurst 1970, Jackson *et al.* 1987, Palmer 1995, Smith and Burger 2005). To allow captive-reared chicks to be used in this manner, researchers often imprint them onto themselves (Kimmel and Healy 1987). Once imprinted, the chicks will forage in the selected brood-rearing habitats and then return to the handlers after a foraging trial. The diet of chicks is then examined, most commonly using crop and gizzard analysis. Although this technique offers a significant improvement in assessing the foraging value of habitats, its reliability is questionable because it is unknown whether captive reared chicks select the same prey as wild chicks.

2.0 AIMS

Here, a comprehensive three-year study of the role of invertebrates in the diet of northern bobwhite chicks was conducted. Within this study, there were four main areas of research: 1) improving the measurement of invertebrate availability to bobwhite chicks; 2) examining the diet and selection of invertebrates by bobwhite chicks; 3) determining the effect of the invertebrate composition in the diet of chicks on growth and survival; 4) assessing the foraging value of genetically modified cotton. The research was divided into four chapters. The specific aims of each chapter were:

CHAPTER III

THE RECOVERY OF INVERTEBRATE DIAGNOSTIC-FRAGMENTS IN THE FAECES OF NORTHERN BOBWHITE CHICKS: IMPLICATIONS FOR DIET DETERMINATION

1). To conduct feeding trials to examine the differential recovery of invertebrate-diagnostic fragments ingested by bobwhite chicks.

2). Using these data, devise correction factors to allow the reconstruction of the invertebrate component of the diet of wild and imprinted bobwhite chicks from faecal samples.

CHAPTER IV

A COMPARATIVE STUDY OF THE DIET AND SELECTION OF INVERTEBRATES BY HUMAN-IMPRINTED AND WILD NORTHERN BOBWHITE CHICKS

1). Examine and compare invertebrate prey selection by human imprinted and wild bobwhite chicks.

CHAPTER V

THE INVERTEBRATE COMPOSITION IN THE DIET OF NORTHERN BOBWHITE CHICKS IN THE SOUTHEASTERN UNITED STATES: IMPLICATIONS FOR GROWTH AND SURVIVAL

1). Identify and compare the invertebrate composition in the diet of bobwhite chicks on agricultural and forested landscapes in the southeastern United States.

2). Examine the effect of bobwhite chick age on the invertebrate composition in the diet of chicks.

3). Examine the effects of invertebrate composition in the diet of chicks on growth and survival.

CHAPTER VI

NORTHERN BOBWHITE CHICK-PREY INVERTEBRATE ABUNDANCE IN GENETICALLY MODIFIED COTTON

1). Examine the abundance of northern bobwhite chick-prey invertebrates in two varieties of genetically modified cotton commonly grown in the southeastern United States.

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CHAPTER II

STUDY SITES

1.0 TALL TIMBERS RESEARCH STATION

Tall Timbers Research Station (henceforth, TTRS) is a 1300 ha former northern bobwhite, *Colinus virginianus*, (henceforth, bobwhite) shooting plantation located 16 km north of Tallahassee in Leon county, northern Florida (30°26′N, 84°16′W). County road 12 divides the area into two, north and south (Figure 2.1). TTRS is now intensively managed as a working plantation for the purpose of research, conservation and education. The predominant land cover type on TTRS is classified as upland pine (Table 2.1, Plate 2.1). Pine species include longleaf, *Pinus palustris*, loblolly, *Pinus taeda*, and shortleaf, *Pinus echinata.* The understory plant species in these areas are characteristic of once highly disturbed land that was used for agriculture (henceforth, old field) and include broomsedge, *Andropogon virginicus*, partridge pea, *Cassia spp.*, lespedeza, *Lespedeza spp.*, ragweed, *Ambrosia artemissifolia*, winged sumac, *Rhus copallina*, and blackberry, *Rubus spp*. The upland pine areas are interspersed by drains, which are low lying areas of land covered with deciduous trees, including mockernut hickory, *Carya tomentosa*, flowering dogwood, *Cornus florida*, and sweetgum, *Liquidambar styraciflua* (Plate 2.2). There is usually little understory vegetation in these areas. Fields are areas that are disked annually in spring to encourage the growth of herbaceous plants and range from 0.01 to 2.5 ha in size (Plate 2.3).

Between March and May each year, approximately 40-50% of the land area was burned in controlled fires. On the north side of TTRS, bobwhite were feed sorghum, *Sorghum bicolour,* year round, either in hoppers or scattered along trails using a tractor and spreader. In 2004, medium sized mammalian predators, including raccoons, *Procyon lotor*, opossums, *Didelphis virginianus*, and coyotes, *Canis latrans*, were trapped and killed on all areas of TTRS from March to September.

Table 2.1. Land cover types on Tall Timbers Research Station in northern Florida, Pebble Hill Plantation in southern Georgia and farmland in central Georgia, United States, 2002-2004.

Study Site	Land cover	Area (%)		
		2002	2003	2004
Tall Timbers Research Station	Unburned Upland Pine	25.5	27.5	21.0
	Burned Upland Pine	27.0	24.5	31.0
	Drain	26.5	26.5	26.5
	Fallow/ Field	5.5	6.0	6.0
	Wetland	4.0	4.0	4.0
	Road	4.0	4.0	4.0
	Other	7.5	7.5	7.5
Pebble Hill Plantation	Unburned Upland Pine	26.5	28.0	27.0
	Burned Upland Pine	36.0	30.0	33.5
	Unburned Planted Pine	9.0	7.0	8.5
	Burned Planted Pine	5.5	7.5	5.0
	Drain	16.0	16.0	16.0
	Fallow/ Field	3.0	3.0	3.0
	Wetland	3.0	3.0	3.0
	Road	3.5	3.5	3.5
	Other	0.5	2.0	0.5
Georgia Farmland	Arable Field	13.5	13.5	-
	Grass Field	12.5	12.5	-
	Planted Pine	23.5	23.5	-
	Deciduous Woodland	33.0	33.0	-
	Marginal/ scrubland	10.0	10.0	-
	Other	7.5	7.5	-

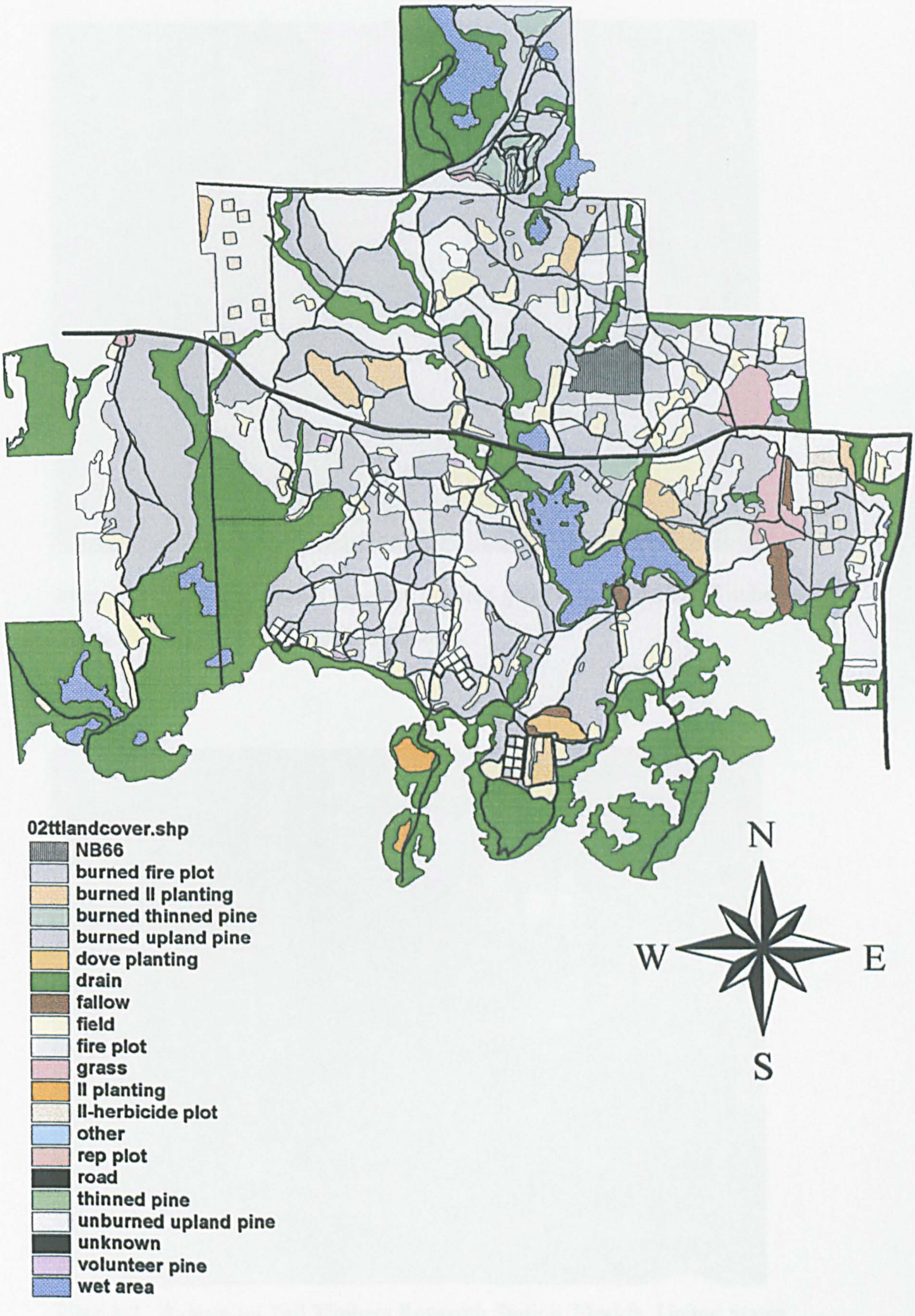

Figure 2.1. Land cover on Tall Timbers Research Station, 2002.

Plate 2.1. An area of upland pine and oldfield ground cover on Tall Timbers Research Station, Florida, United States.

Plate 2.2. A drain on Tall Timbers Research Station, Florida, United States.

Plate 2.3. An annually disked field on Tall Timbers Research Station, Florida, United States.

2.0 PEBBLE HILL PLANTATION

Pebble Hill Plantation (henceforth, PH) is located approximately 13 km northeast of TTRS in Grady and Thomas counties in southern Georgia (30°50′N, 83°58′W). PH is a 1200 ha former bobwhite shooting estate now intensively managed by TTRS (Figure 2.2). Blackshear road divides PH into two halves, north and south. As on TTRS, upland pine with an under story of old field vegetation is the predominant land cover. However, approximately 20% of PH is upland pine with undisturbed, native ground cover with species such as wiregrass, *Aristida stricta* and *A. beyrichiana*, bracken fern, *Pteridium aquilinum*, and runner oak, *Quercus pumila* (Table 2.1, Plate 2.4).

Similarly to TTRS, 40-50% of PH was burned between March and May each year. Sorghum was fed to bobwhite year round on the south side of PH in either hoppers and/ or scattered along trails using a tractor and spreader. Most fields were disked in spring and were 0.03-3.8 ha in size. In 2001-2003, mid-sized mammals (same species as on TTRS) were trapped and killed on all PH from March to September.

Plate 2.4. An area of undisturbed native groundcover (predominately wiregrass) on Pebble Hill Plantation, Georgia, United States.

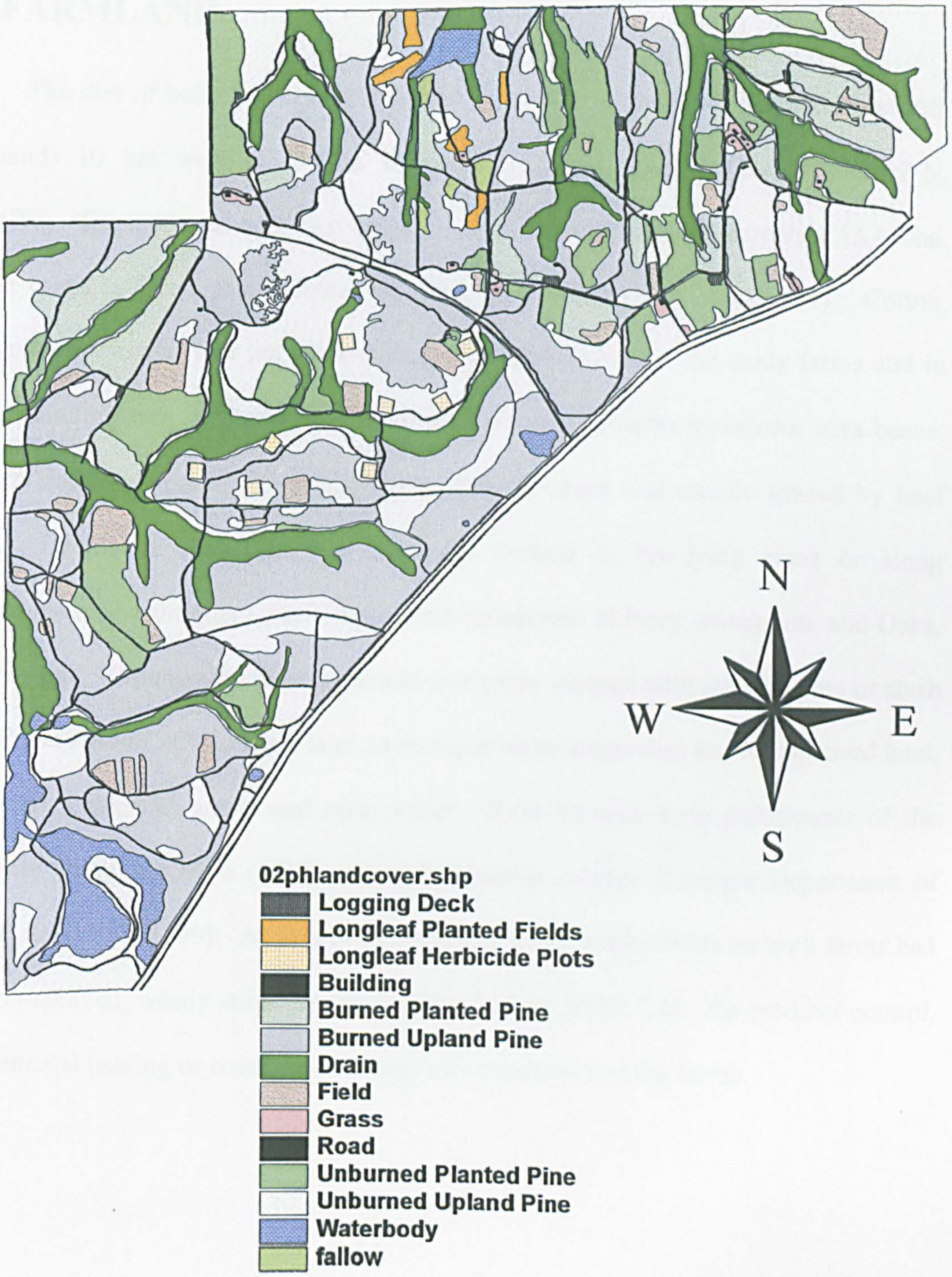

Figure 2.2. Land cover on Pebble Hill Plantation, 2002.

3.0 FARMLAND

The diet of bobwhite chicks was studied on and around two farms (henceforth, Farmland) 10 km west of Dublin in Laurens county, central Georgia (32°32′N, 82°54′W). The total area on which bobwhite were studied was approximately 13,440ha. Arable crops or grass were planted on 26% of the study area (Table 2.1). Cotton, *Gossypium hirsutum*, was the predominant crop type grown on the study farms and in the surrounding area. Other crops grown were peanuts, *Arachis hypogaea*, soya beans, *Glycine max*, and maize, *Zea mays*, (Plate 2.5). Pasture was usually grazed by beef cattle. Deciduous woodland was primarily located in low-lying areas or along watercourses. Predominant tree species were mockernut hickory, sweetgum, and Oaks, *Quercus spp.*. Commercial pine woodland was either planted with loblolly pine or slash pine, *Pinus elliottii*. Other main land cover types were hedgerows and unimproved land, roads and residential areas, and open water. Both farmers were participants of the Bobwhite Quail Initiative (BQI) agri-environmental scheme (Georgia Department of Natural Resources 1999). As part of this scheme, some arable fields on both farms had 6m, non-sprayed, weedy strips around their perimeters (Plate 2.6). No predator control, supplemental feeding or controlled burning was conducted on the farms.

Plate 2.5. Row crops, such as maize, are commonly grown on farms in central Georgia, United States.

Plate 2.6. A 6m Bobwhite Quail Initiative (BQI) conservation border surrounding an arable field in central Georgia, United States.

4.0 REFERENCES

Georgia Department of Natural Resources. 1999. The Bobwhite Quail Initiative: restoring Georgia's state game bird. Georgia Department of Natural Resources, Wildlife Resources Division, Social Circle, Georgia, USA.

CHAPTER III

THE RECOVERY OF INVERTEBRATE DIAGNOSTIC-FRAGMENTS IN THE FAECES OF NORTHERN BOBWHITE CHICKS: IMPLICATIONS FOR DIET DETERMINATION

SUMMARY

Faecal analysis is a commonly used technique for assessing the diet of birds. However, due to the differential recovery of diagnostic-fragments of invertebrates, it is necessary that the numbers found in the faeces be adjusted to reveal each prey items' contribution in the diet. In this study, a feeding trial was conducted to examine differential recovery of various invertebrate-diagnostic fragments in the faeces of northern bobwhite chicks.

Beginning at 07:30, five different invertebrate prey items were fed to 10-day-old northern bobwhite chicks at five different times of the day. Their faeces were collected hourly until 08:30 the following morning and then examined for invertebrate-diagnostic fragments. The proportions of diagnostic fragments recovered to those ingested were calculated over two time periods, 1) from 07:30 to 08:30 the following morning (total) and 2) from 21:30 to 06:30 the following morning (roost). The 'roost' time period was chosen to represent the time wild bobwhite broods spend at a nocturnal roost site.

For both collection periods, differences in recovery proportions among invertebrate-diagnostic fragments were found. The recovery proportions of Coleoptera tibia were often double those for Lepidoptera mandibles. Consequently, to allow the diet of bobwhite chicks to be reconstructed from feacal examinations, adjustment values were calculated for each invertebrate-diagnostic fragment.

The results of this study show that it is important that the numbers of diagnostic fragments recovered in the faeces are adjusted to reflect those ingested, otherwise, the contribution of some invertebrates to the diet of bobwhite chicks could be seriously underestimated.

1.0 INTRODUCTION

An understanding of the dietary needs of an animal is a key facet in determining its habitat requirements and ultimately how food resources within a habitat affect populations. Studies of bird-diets have used both lethal and non-lethal techniques to collect samples for dietary analysis (Rosenberg and Cooper 1990). Many studies have examined the digestive tracts (crops and/ or gizzards) collected from birds killed by hunters (Potts 1970, Pulliainen 1984, Curtis *et al.* 1990), scientists (Stoddard 1931, Hurst 1972, Erikstad and Spidsø 1982, Drut *et al.* 1994, Krapu *et al.* 2004) or found dead (Ford *et al.* 1938). To provide digestive tracts for dietary analysis, the killing of gamebirds or waterfowl outside of their respective hunting seasons, or non-hunted birds at anytime, may be difficult to warrant on both legal (inability to obtain the necessary licenses) and ethical grounds, particularly if collection could harm small local populations. Although the use of ligatures and chemical emetics can offer non-lethal methods for collecting samples for dietary analysis (Rosenberg and Cooper 1990), the capture, handling, and treatment involved makes these techniques intrusive and has caused the death of some birds in a few studies (Davies 1976, Johnson *et al.* 1980, Johnson *et al.* 2002). The use of faecal matter, however, offers a non-invasive technique that has been widely used in dietary studies of birds, particularly gamebirds (grey partridge, *Perdix perdix* [Green 1984], red-legged partridge, *Alectoris rufa* [Green 1984], ring-necked pheasant, *Phasianus colchicus* [Hill 1985, Draycott *et al.* 1999] capercaillie, *Tetrao urogallus* [Picozzi *et al.* 1999], and red grouse, *Lagopus lagopus scoticus* [Butterfield and Coulson 1975, Park *et al.* 2001]), and passerines (blue tit, *Parus caeruleus* [Pulido and Díaz 1994], corn bunting, *Miliaria calandra* [Brickle and

Harper 1999] skylarks, *Alauda arvensis* [Green 1980, Poulsen *et al.* 1998], dunnock, *Prunella modularis* [Moreby and Stoate 2001], pied wagtail, *Motacilla alba yarrellii* [Davies 1976] whitethroat, *Sylvia communis* [Moreby and Stoate 2001], and yellowhammer, *Emberzia citronella* [Moreby and Stoate 2001]).

In chick-diet studies, altricial chick faecal matter is most often collected from the nest site (Poulsen *et al.* 1998, Brickle and Harper 1999, Moreby and Stoate 2001), whereas samples from precocial chicks are either obtained during handling after capture (Green *et al.* 2000, Park *et al.* 2001), from diurnal loafing sites where chicks have been flushed (Moreby *et al.* 1999) or at nocturnal roost sites (Green 1984, Hill 1985, Picozzi *et al.* 1999). The collection of faeces at nocturnal roost sites is usually conducted when brooding adults are fitted with a radio-transmitter and can therefore be located using radio-telemetry (Green 1984, Hill 1985).

Faecal matter collected from young birds is often analysed using a method similar to that described by Moreby (1988). Firstly, fine debris and uric acid that can cloud a sample and hamper identifying invertebrate-diagnostic fragments are removed by washing the faecal material through a fine sieve. Samples are then systematically examined under a binocular microscope to determine the invertebrates present. Invertebrate-diagnostic fragments, those quantifiable invertebrate parts (carried in known numbers) that often remain intact e.g. mandibles, tibias and femurs, are identified and counted using published illustrations (e.g. Peterson 1960, 1962), photographic guides (e.g. Ralph *et al.* 1985, Moreby 1988) and reference collections of whole invertebrates. The minimum number of individual invertebrates that must have been ingested to account for the diagnostic fragments found can then be calculated.

Aside from the technical expertise and time required to analyse the highly fragmented faecal samples, differential rates of recovery of different invertebrate items in faeces can cause serious biases (Rosenberg and Cooper 1990). Therefore, to relate the number of individual invertebrates found in the faeces to those ingested, correction factors have been developed for various bird species, including blue tit (Pulido and Díaz 1994), grey partridge (Green 1984), skylark (Green 1978), snow bunting, *Plectrophenax nivalis* (Custer and Pitelka 1974), and stone curlew, *Burhinus oedicnemus* (Green and Tyler 1989). Correction factors are often calculated through feeding trials where known numbers of individual prey items are fed to birds and then the faeces, collected over a specific time period, are examined to determine the percentage recovery of individual prey items or diagnostic fragments.

Incubator-hatched gamebird chicks either fostered onto a domestic bantam hen or imprinted onto a human are increasingly being used to assay the value of habitats for wild foraging broods (Hurst 1972, Jackson *et al.* 1987, Healy 1985, Kimmel and Healy 1987, Spidsø and Stuen 1988, Palmer 1995). The background and methodology of using human-imprinted chicks (henceforth, imprinted chicks) to measure invertebrate availability in a habitat is discussed in more detail in Chapter IV. Previously, researchers have generally followed a method similar to that described by Palmer *et al.* (2001) who allowed the northern bobwhite, *Colinus virginianus*, (henceforth, bobwhite) chicks to forage for 30 minutes, euthanizing them and then examining the crop and gizzard contents for ingested prey items. Alternatively, to avoid euthanizing chicks, their faecal matter could be collected after foraging and analysed using the method described above. However, by employing faecal analysis, the numbers of invertebrates found must be adjusted for differential recovery to allow comparisons to be made between imprinted chick trials conducted at different times of the day and also between diets of imprinted and wild chicks. Green and Tyler (1989) described a formula using expected diagnostic-fragment recovery rates to reconstruct the diet of birds from faecal analysis. If f is the number of diagnostic-fragments recovered in the faeces per invertebrate eaten and there are a total of K invertebrate types, then the proportion Pj, in the diet by numbers of invertebrate type j, from a faecal sample will be given by:

$$Pj = \frac{(n_j/f_j)}{\sum_{i=1}^{K} (n_i/f_i)}$$

Where n are the counts of invertebrate diagnostic-fragments for the different invertebrate types. If more than one diagnostic-fragment from an invertebrate type is counted in a faecal sample, e.g. 3 tibia and 2 femur from a coleopteran invertebrate, the fragment yielding the highest value of (n/f) could be taken and the others dismissed.

Here, feeding trials were conducted to examine the differential recovery of invertebrate-diagnostic fragments ingested by bobwhite chicks. These data were then used to calculate correction factors to allow the invertebrate component of the diet of wild and imprinted bobwhite chicks to be reconstructed from faecal samples.

2.0 METHODS

In 2002, 150 bobwhite eggs from wild strain captive birds were hatched in an incubator (G.Q.F., Savannah, Georgia). One hundred chicks that hatched within a few hours of each other were selected and imprinted onto a human according to Palmer *et al.* (2001). Chicks were housed at a constant temperature (35 °C) and provided with commercial gamebird chick food (Purina Mills, Inc., St. Louis, Missouri), grit and vitamin supplemented water *ad libitum*. Until seven days of age, the chicks were also fed mealworms, *Tenebrio molitor,* to facilitate imprinting and acceptance of invertebrate prey during the trial.

At seven days of age, 80 imprinted chicks were randomly assigned to 40 pens, two per pen. Pairs of imprinted chicks were used to alleviate stress caused by isolation (Moreby *et al.* 2006) and handling, as the effect of stress can make the results of feeding trials difficult to interpret (Levey and Karasov 1994). Each pair of chicks was given unique colour coded marks using felt-tipped pens on their chests to identify them to a pen. The pens were constructed within five chick brooders (G.Q.F., Savannah, Georgia), each pen being 34cm x 23cm x 24cm in size (Plate 3.1), and constructed from wire mesh and the walls were lined with white paper. The floor of each pen was also constructed of wire mesh: this allowed faeces to fall on to a collecting plate below. The collecting plates were aluminium trays marked with indexed grids to correspond with each pen. There were two trays for each brooder so when one was removed to collect the faecal samples, it could be immediately replaced with the other to prevent any loss of faeces. A wire mesh roof was placed on each brooder. The chicks were housed at a constant temperature of 35 °C using thermostat regulated heat lamps.

Plate 3.1. Chicks were housed in pens with wire mesh floors to allow faeces to be collected from a metal tray below.

The temperature within each pen was checked regularly using thermometers located in each pen. Chicks were provided commercial gamebird chick food, grit and vitamin supplemented water *ad libitum*. Between 06:30 and 07:00 each morning, the main lights in the room housing the chicks were turned on. These remained on until between 21:00 to 21:30. Small red 'brooding' lights located over the pens remained on 24 hours.

Invertebrates for the trial were collected using a D-Vac® suction insect sampler (D-Vac Company, Ventura, California) and by sweep netting one to two days prior to the trial. Invertebrates were kept frozen until the trial. Five invertebrate groups from five different orders, Araneae, Coleoptera, Hemiptera, Lepidoptera (larvae), and Orthoptera were selected for the trial (Table 3.1). Wild bobwhite chicks often eat the invertebrates selected for this trial, as reported in Chapter V. The number of individual invertebrates offered to each pair of chicks was dependent on availability. At each feeding, each pair of chicks was offered ten Araneae, twelve Coleoptera, seven Hemiptera, two Lepidoptera Larvae, and seven Orthoptera. The variation in size of individuals within taxonomic groups was kept to a minimum.

Table 3.1. The taxa, size and diagnostic fragments of invertebrates offered in the feeding trial.

Order	Family	Size (mm)	Diagnostic fragments
Araneae	Oxyopidae	15-20	Fang
Coleoptera	Chrysomelidae	5-6	Tibia, Femur, Mandible
Hemiptera	Lygaeidae	8-10	Front Tibia, Clavus
Lepidoptera (larvae)	Various	15-20	Mandible
Orthoptera	Acrididae	15-20	Mandible

The feeding trial was conducted when the chicks were ten days old, thereby allowing the chicks three days to acclimatize to their pens. Each pen was randomly assigned one of five feeding sequences (eight pens per sequence). The feeding sequences were:

1) Lepidoptera Larvae, Orthoptera, Hemiptera, Coleoptera, Araneae
2) Araneae, Lepidoptera Larvae, Orthoptera, Hemiptera, Coleoptera
3) Coleoptera, Araneae, Lepidoptera Larvae, Orthoptera, Hemiptera
4) Hemiptera, Coleoptera, Araneae, Lepidoptera Larvae, Orthoptera
5) Orthoptera, Hemiptera, Coleoptera, Araneae, Lepidoptera Larvae

At each feeding time chicks received their appropriate invertebrate order for that feeding. Invertebrates were given to chicks in small Petri dishes placed on a white paper towel to prevent invertebrates falling through the floor of the pen. There were five, one hour feeding times through the day, 07:30-08:30 (early morning), 10:30-11:30 (late morning), 15:30-16:30 (mid afternoon), 18:30-19:30 (late afternoon) and, 20:30-21:30 (evening). To increase the likelihood of chicks ingesting the invertebrates, the commercial chick food was removed 30 minutes prior to each feeding. After each feeding, the Petri dishes and paper towels were carefully removed from each pen and the commercial chick food replaced.

Faeces from each pen were collected initially at 07:30 and then every hour for 25 hours. Faeces were carefully removed from the trays using small scrapers and tweezers. Dried faeces were removed with the aid of a small amount of water. Any faecal matter that remained in the pens, including in the drinkers and food trays, was also carefully removed. The Petri dishes and towels used to feed the trial invertebrates were also carefully checked for faecal matter. Collection of faeces from the trays, towels and Petri dishes was done in a neighbouring room to minimize disturbance to the chicks. All faecal matter from each pen, for each hour, was placed in separate small plastic containers, filled with 70% alcohol, and labeled with the collection time and pen number. After the last feeding at 21:30, the main lights were turned out in the room, although the small red brooding lights located over each pen were left on. These lights emitted enough light over each pen to enable researchers to change the collection trays and check for faecal matter in the pens each hour during the night. At 06:30 the main lights in the room were turned back on.

Under a binocular microscope (25-40 x magnification), each faecal sample was carefully flushed out of its container using 70% alcohol into a Petri dish marked with a 1 cm × 1 cm grid. The contents of the Petri dish were broken down with a metal pointer and then systematically searched for invertebrate-diagnostic fragments and other remains. The diagnostic fragments counted for each invertebrate type are described in Table 3.1 and were identified using a reference collection.

2.1 Statistical Analysis

As in other feeding trials, where the recovery rates of diagnostic fragments rather than individual prey were calculated (Green and Tyler 1989, Jenni *et al.* 1990), it was assumed that the recovery of diagnostic fragments from individual invertebrates were independent. This is probably valid as prey items become highly fragmented during digestion.

Analysis was based on the proportions of diagnostic fragments recovered in the faeces from those ingested. Therefore for each feeding period, pens were only included in the analysis when at least one prey item was ingested. The recovery of diagnostic fragments over two time periods, 'Total' (from feeding until 08:30 the following morning) and 'Roost' (from 21:30 until 06:30 the following morning), were examined. The 'Roost' time period was chosen to represent the time wild broods spend at a nocturnal roost site. Proportions were arcsine transformed before analysis. Within each feeding period (1-5), differences in recovery rates among the diagnostic fragments were examined using ANOVA. Due to the large number of comparisons, a Bonferroni adjustment was used. All analyses were conducted using Systat 8.0 (SPSS Inc. 1998).

2.1.1 Diet reconstruction

In order to use the formula described by Green and Tyler (1989) (see introduction above) for reconstructing the diet of imprinted and wild bobwhite chicks using faecal analysis, the number of diagnostic-fragments recovered per invertebrate ingested (f) was calculated using the mean recovery proportions. For imprinted chicks, the total recovery data from feeding periods 2, 3 and 4 were used to calculate f for foraging trials conducted in the morning, afternoon or evening, respectively. To simulate the recovery of diagnostic fragments from invertebrates eaten throughout the day by wild chicks, the f values for faeces collected from nocturnal roost sites were calculated from the pooled (feeding periods 1-5) roost recovery data.

3.0 RESULTS

3.1 Invertebrate ingestion

Of a total of 1520 invertebrates offered to the chicks, 1160 (76.3%) were eaten. Although the proportions of Araneae, Hemiptera, Lepidoptera larvae and Orthoptera eaten from those offered did not differ significantly between feeding periods, the proportions of Coleoptera did ($F_{4,35} = 2.717$, $P = 0.045$) (Figure 3.1).

3.2 Recovery of diagnostic fragments

3.2.1 Total recovery

Differences in total recovery rates among diagnostic fragments were found for feeding periods 3 ($F_{7,55} = 3.727$, $P = 0.002$) and 4 ($F_{7,55} = 2.655$, $P = 0.019$) (Table 3.2). Whilst the proportions of Coleoptera tibia recovered for each feeding period were in the range of 50-65%, the recovery proportions of Lepidoptera larvae mandibles were only half this (28-32%). The proportions of Araneae fangs, Coleoptera femurs, Coleoptera mandibles, Hemiptera front tibias and Orthoptera mandibles recovered did not differ within any of the feeding periods. Differences in total recovery rates among diagnostic fragments were also found when the feeding periods were pooled ($F_{7,299} = 7.115$, $P = <0.001$) (Table 3.2).

3.2.2 Roost recovery

Data were too sparse to examine differences in roost recovery rates among diagnostic fragments for feeding periods 1-3 as few diagnostic fragments were expelled during the roost period (Figures 3.2–3.4). Figures 3.5 and 3.6 show that diagnostic fragments from invertebrates fed at feeding periods 4 and 5 were continually expelled during the roost period. Differences were found in roost recovery rates among diagnostic fragments for feeding period 4 ($F_{7,55} = 3.8$, $P = 0.002$) and when the feeding periods were pooled ($F_{7,299} = 4.943$, $P = <0.001$) (Table 3.3). Significantly greater proportions of Coleoptera tibias were recovered from these feeding periods than Lepidoptera larvae mandibles and Orthoptera mandibles.

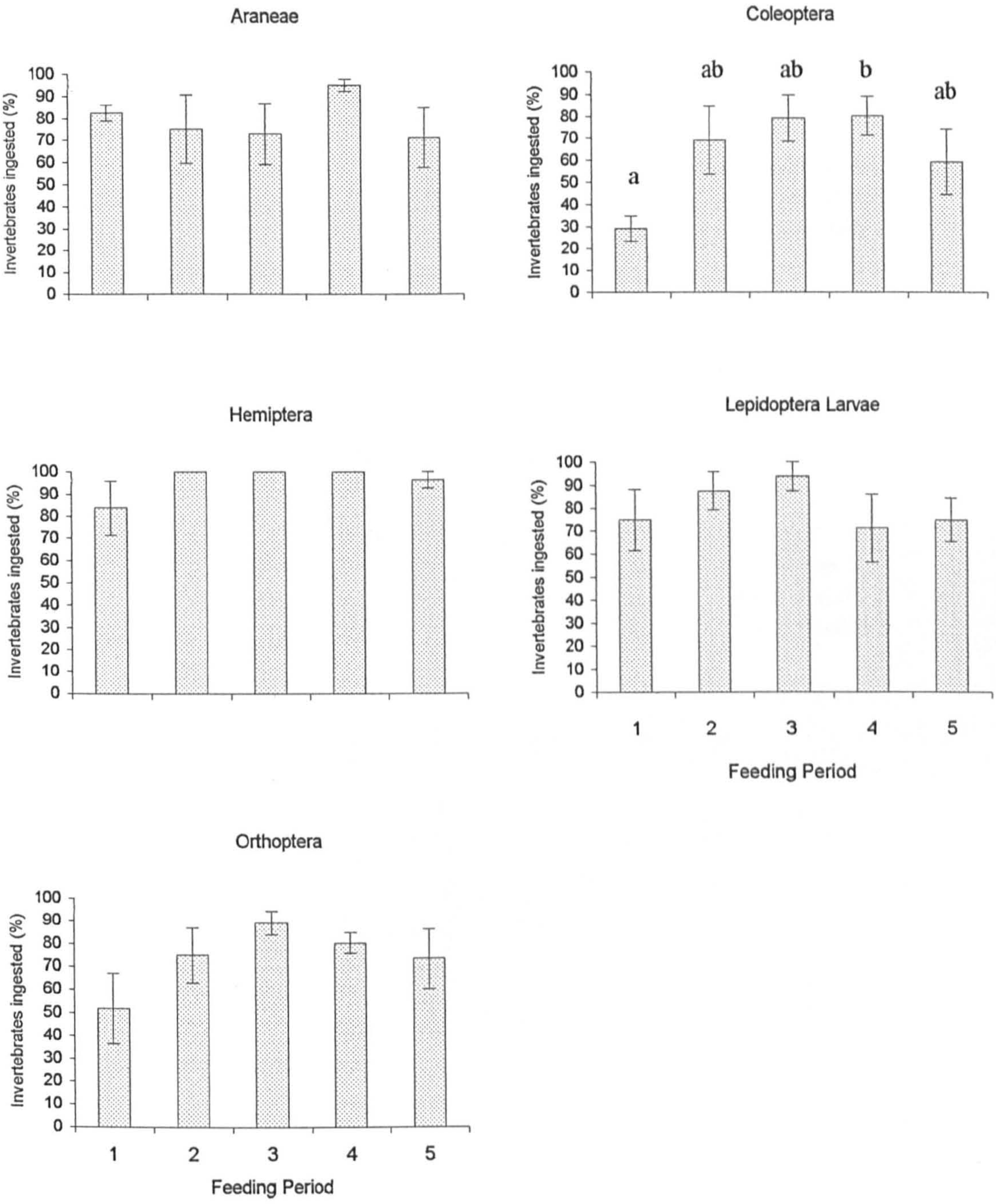

Figure 3.1. The mean proportions (%) (±SE) of those invertebrates offered to 10 day-old northern bobwhite chicks that were ingested during five feeding periods; 1 = 07.30-08.30, 2 = 10.30-11.30, 3 = 15.30-16.30, 4 = 18.30-19.30, 5 = 20.30-21.30. In each feeding period, known numbers of each invertebrate group were fed to 8 different pens (40 pens in total) (*n* = 8). Each pen contained two chicks. Only one invertebrate group was offered to each pen, during each feeding period. Data were arcsine transformed before analysis. Means with the same letter do not differ at the 5% level of significance (Bonferroni Comparison).

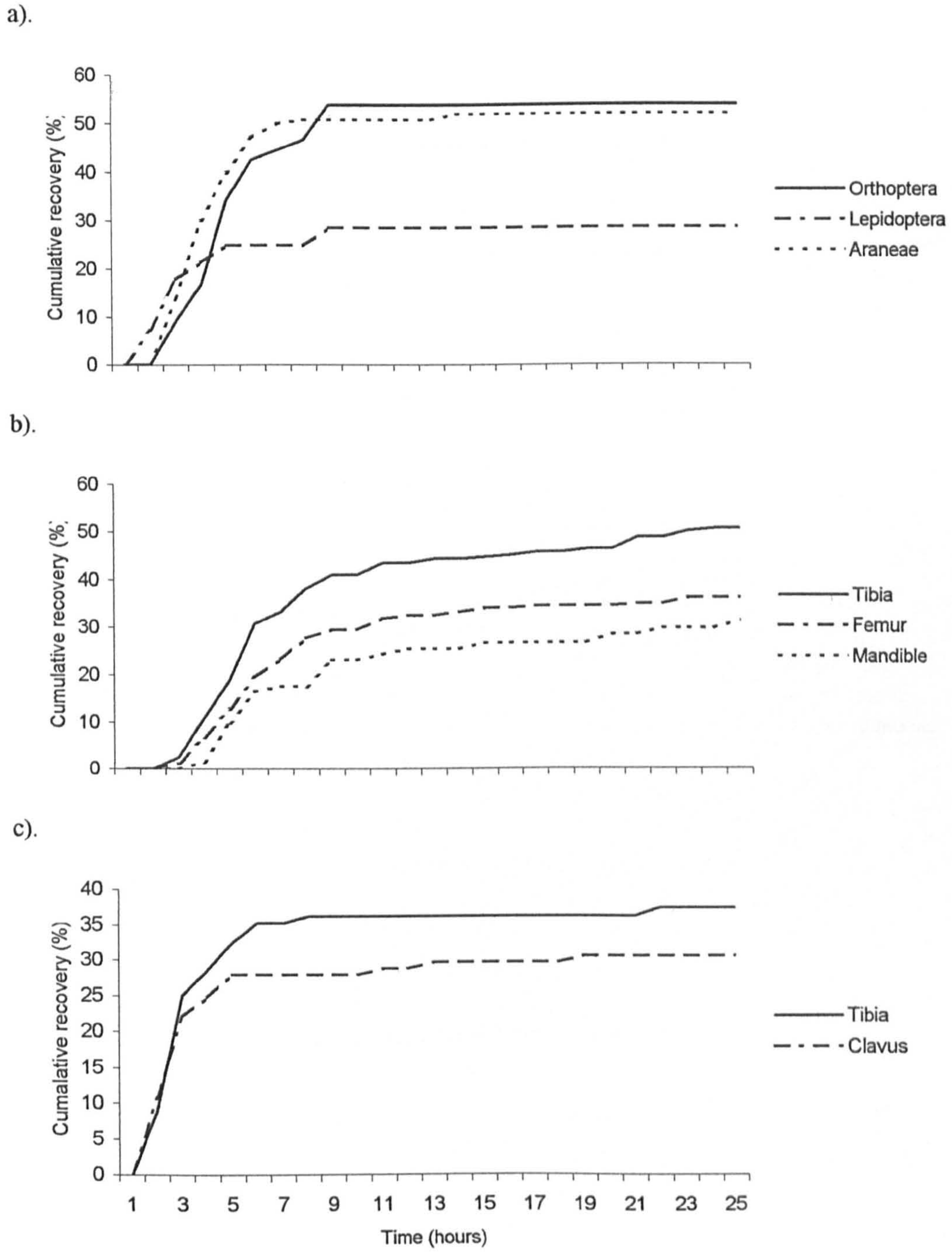

Figure 3.2. Cumulative percentage of invertebrate diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected hourly for 25 hours after being fed prey items at 07:30-08:30. a). Recovery of Orthoptera mandibles (*n* = 7), Lepidoptera mandibles (*n* = 7) and Araneae fangs (*n* = 8). b). Recovery of Coleoptera tibia, femur, and mandibles (*n* = 7). c). Recovery of Hemiptera front tibia and clavus (*n* = 8). *n* = number of pens (2 chicks/pen).

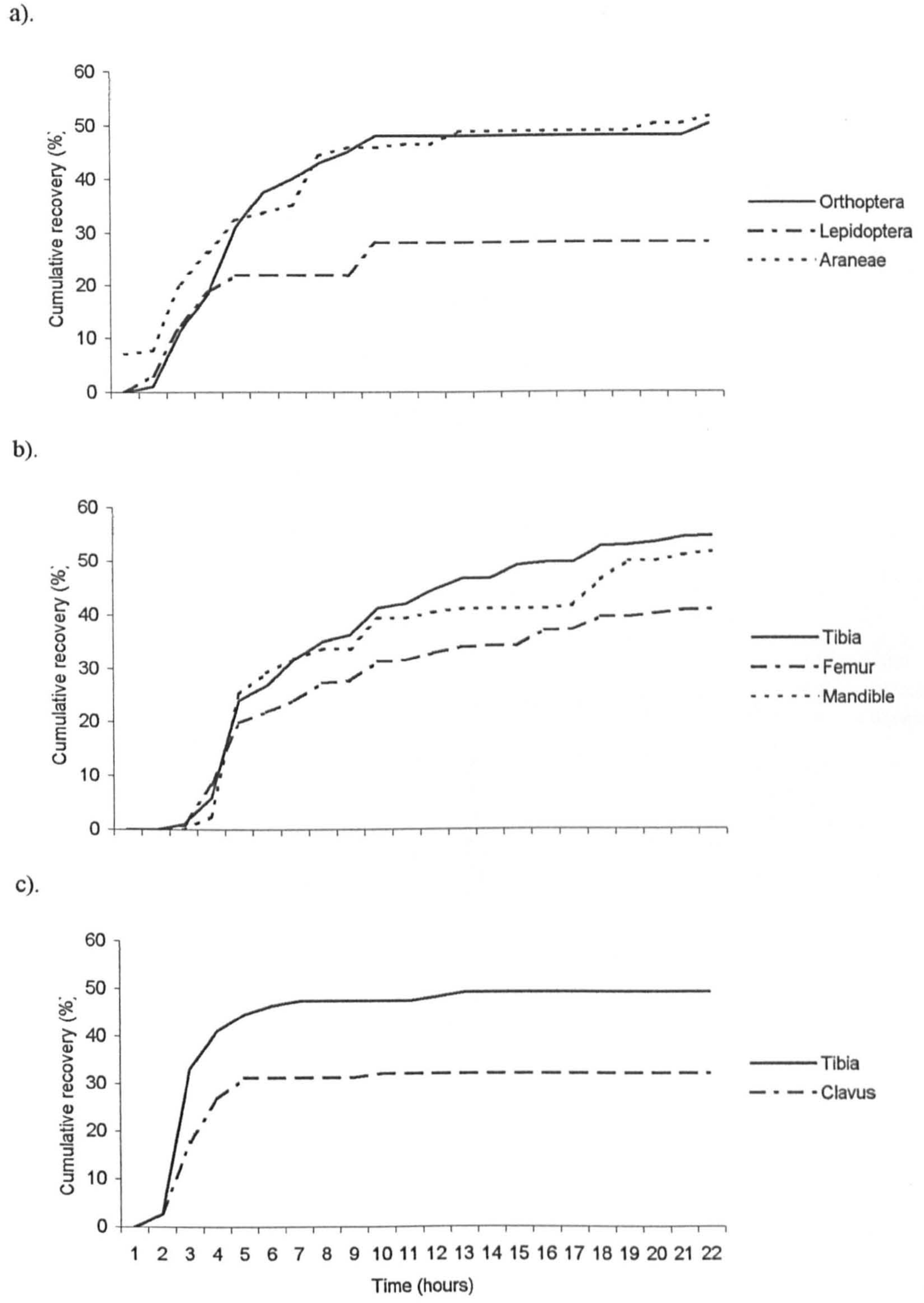

Figure 3.3. Cumulative percentage of invertebrate diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected hourly for 22 hours after being fed prey items at 10:30-11:30. a). Recovery of Orthoptera mandibles (*n* = 7), Lepidoptera mandibles (*n* = 8) and Araneae fangs (*n* = 7). b). Recovery of Coleoptera tibia, femur and mandibles (*n* = 7) c). Recovery of Hemiptera front tibia and clavus (*n* = 8). *n* = number of pens (2 chicks/pen).

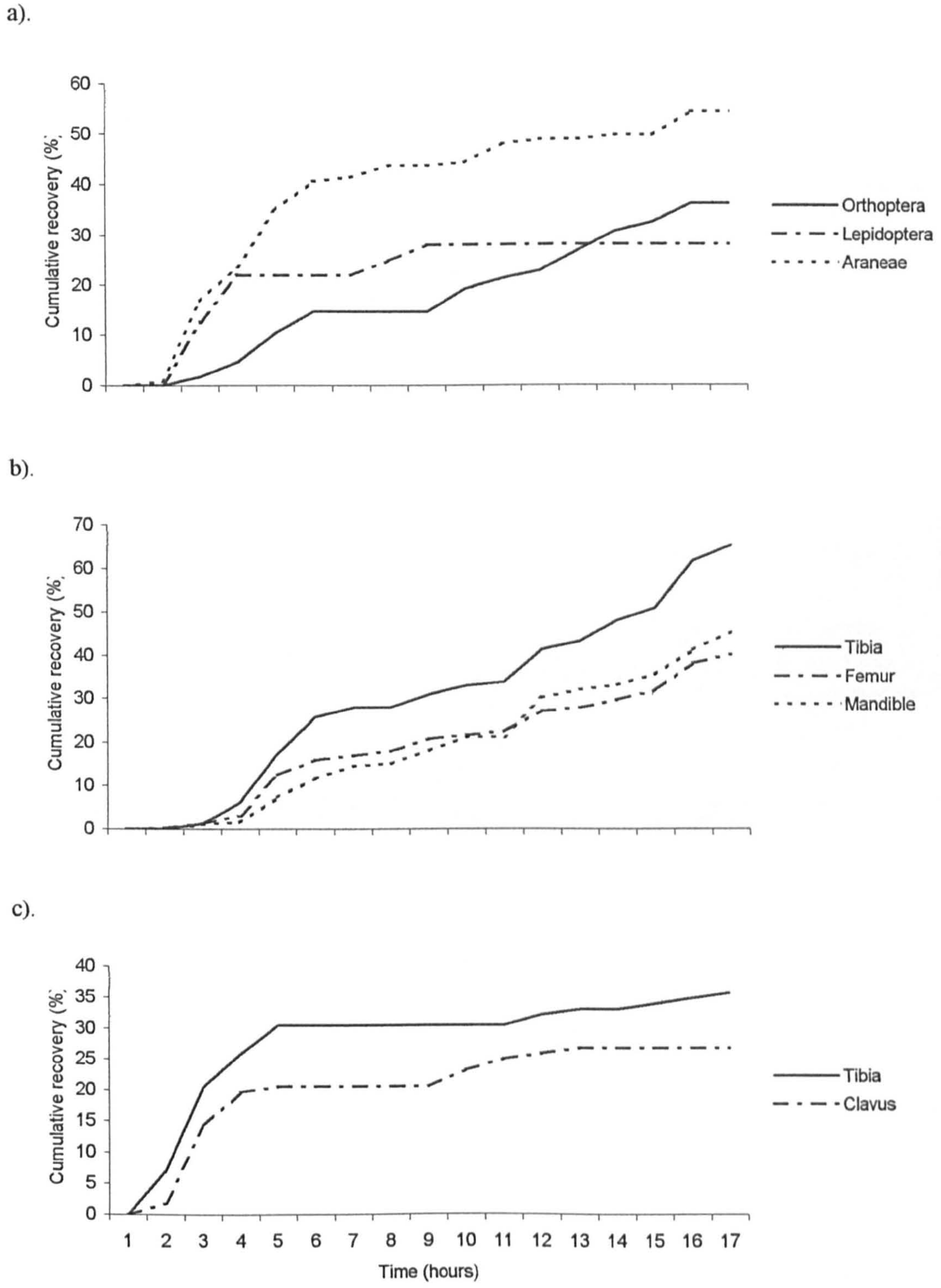

Figure 3.4. Cumulative percentage of invertebrate diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected hourly for 17 hours after being fed prey items at 15:30-16:30. a). Recovery of Orthoptera mandibles (*n* = 8), Lepidoptera mandibles (*n* = 8) and Araneae fangs (*n* = 7). b). Recovery of Coleoptera tibia, femur and mandibles (*n* = 8). c). Recovery of Hemiptera front tibia and clavus (*n* = 8). *n* = number of pens (2 chicks/pen).

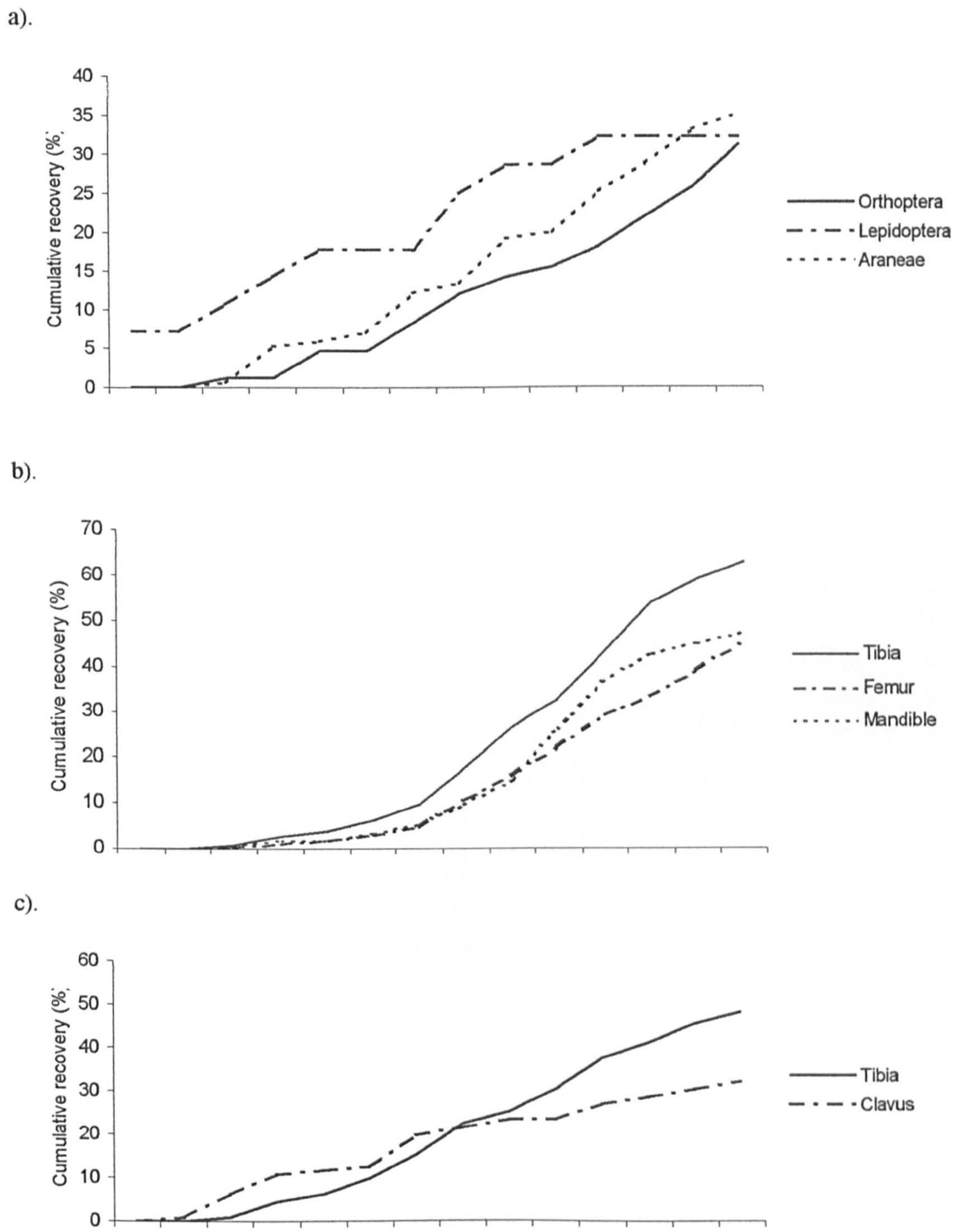

Figure 3.5. Cumulative percentage of invertebrate diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected hourly for 14 hours after being fed prey items at 18:30-19:30. a). Recovery of Orthoptera mandibles (*n* = 8), Lepidoptera mandibles (*n* = 7) and Araneae fangs (*n* = 8). b). Recovery of Coleoptera tibia, femur and mandibles (*n* = 8). c). Recovery of Hemiptera front tibia and clavus (*n* = 8). *n* = number of pens (2 chicks/pen).

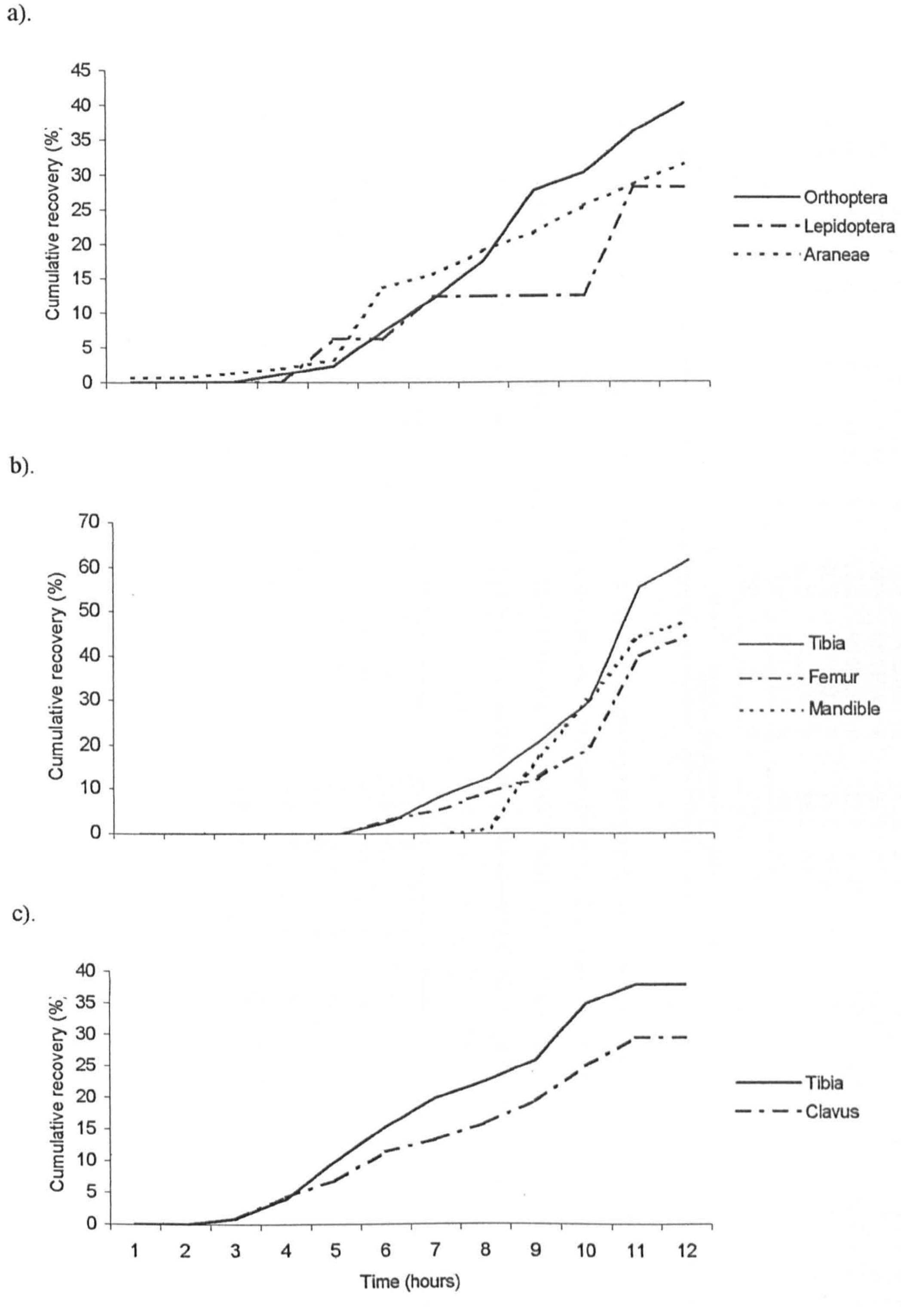

Figure 3.6. Cumulative percentage of invertebrate diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected hourly for 12 hours after being fed prey items at 20:30-21:30. a). Recovery of Orthoptera mandibles (*n* = 7), Lepidoptera mandibles (*n* = 8) and Araneae fangs (*n* = 8). b). Recovery of Coleoptera tibia, femur and mandibles (*n* = 8). c). Recovery of Hemiptera front tibia and clavus (*n* = 8). *n* = number of pens (2 chicks/pen).

Table 3.2. Mean proportion (%) (±SE) of invertebrate-diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected up until 08:30 the following morning after ingestion. Feeding periods; 1 = 07.30-08.30, 2 = 10.30-11.30, 3 = 15.30-16.30, 4 = 18.30-19.30, 5 = 20.30-21.30. *n* = number of pens (2 chicks/pen). Analysis conducted on arcsine-transformed data. Within each feeding period means with the same letter do not differ at the 5% level of significance (Bonferroni adjustment).

Invertebrate / Fragment counted	Feeding period																	
	1			2			3			4			5			Pooled		
	n	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Araneae / Fang	8	51.34	6.78	7	51.75	10.38	7	54.33 ab	6.75	8	35.14 ab	5.98	8	31.53	6.29	38	44.38 ab	3.45
Coleoptera / Tibia	7	50.52	5.64	7	54.60	8.36	8	65.15 a	4.14	8	62.61 a	2.17	8	61.38	7.99	38	59.18 a	2.69
Coleoptera / Femur	7	35.87	4.01	7	40.95	9.44	8	40.07 ab	4.06	8	45.56 ab	4.29	8	44.72	9.49	38	41.59 ab	2.91
Coleoptera / Mandible	7	30.95	7.29	7	51.67	11.85	8	45.15 ab	7.42	8	47.39 ab	3.32	8	47.91	12.18	38	44.79 ab	3.95
Hemiptera / Front Tibia	8	37.32	7.66	8	49.11	5.95	8	35.71 ab	5.23	8	48.21 ab	7.84	8	37.86	7.26	40	41.64 b	3.05
Hemiptera / Clavus	8	30.54	5.52	8	32.14	3.82	8	26.79 b	4.43	8	32.14 ab	9.06	8	29.46	7.45	40	30.21 bc	2.71
Lepidoptera larvae / Mandible	7	28.57	10.10	8	28.13	10.68	8	28.13 b	9.95	7	32.14 b	11.85	8	28.12	12.89	38	28.95 c	4.17
Orthoptera / Mandible	7	53.83	13.81	7	50.34	7.64	8	36.16 ab	4.89	8	31.19 ab	6.14	7	35.99	7.07	37	41.08 ab	3.77

Table 3.3. Mean proportion (%) (±SE) of invertebrate-diagnostic fragments recovered in the faeces of 10 day-old northern bobwhite chicks collected between 21:30 and 06:30 the night after ingestion. Collection period simulates the time wild broods spend at a nocturnal roost site. Feeding periods; 1 = 07.30-08.30, 2 = 10.30-11.30, 3 = 15.30-16.30, 4 = 18.30-19.30, 5 = 20.30-21.30. *n* = number of pens (2 chicks/pen). Analysis conducted on arcsine-transformed data. Data were not analysed for periods 1-3 as data were too sparse. Within each feeding period means with the same letter do not differ at the 5% level of significance (Bonferroni adjustment).

Invertebrate / Fragment counted	Feeding period																	
	1			2			3			4			5			Pooled		
	n	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Araneae / Fang	8	0	0	7	3.73	1.90	7	8.90	2.50	8	28.11 ab	6.60	8	24.83	5.14	38	13.48 ac	2.58
Coleoptera / Tibia	7	5.83	2.84	7	11.47	5.22	8	25.04	2.98	8	52.87 a	3.73	8	29.47	8.42	38	25.79 a	3.47
Coleoptera / Femur	7	2.78	1.82	7	8.61	4.25	8	15.88	3.63	8	33.20 ab	3.36	8	19.29	7.87	38	16.49 ac	2.64
Coleoptera / Mandible	7	4.17	2.73	7	10.60	5.33	8	24.03	4.78	8	41.96 ab	3.25	8	29.97	15.40	38	22.92 ad	4.09
Hemiptera / Front Tibia	8	1.25	1.25	8	1.79	1.17	8	3.57	2.70	8	40.18 ab	6.60	8	34.82	6.39	40	16.32 ac	3.34
Hemiptera / Clavus	8	0.89	0.89	8	0	0	8	6.20	2.84	8	22.32 b	8.26	8	25.00	7.64	40	10.89 ac	2.79
Lepidoptera larvae / Mandible	7	0	0	8	0	0	8	6.25	4.09	7	21.43 b	8.50	8	12.50	8.18	38	7.90 c	2.68
Orthoptera / Mandible	7	0	0	7	0	0	8	17.93	3.17	8	20.71 b	5.87	7	30.17	3.92	37	14.06 cd	2.48

3.3 Diet reconstruction

Using the recovery data from this trial, the number of diagnostic fragments that would be recovered per invertebrate ingested (f) by a bobwhite chick was calculated (Table 3.4). Recovery rates were calculated according to when the faecal samples are collected.

Table 3.4. The number of diagnostic fragments that were recovered per invertebrate ingested from the faeces of 10 day-old northern bobwhite chicks. These can be applied to chick-prey invertebrates of wild or human-imprinted northern bobwhite chicks when calculating (see text) diet composition from faecal analysis using the formula described by Green and Tyler (1989).

Invertebrate group	Fragment counted	Applied to	Recovery per invertebrate (f)			
			Wild chicks[b]	Human-imprinted chicks[c]		
			Roost	Morning	Afternoon	Evening
Coleoptera	Tibia	All Coleoptera[a]	1.55	3.28	3.91	3.76
Coleoptera	Femur	All Coleoptera,	0.99	2.46	2.40	2.73
Coleoptera	Mandible	All Coleoptera,	0.46	1.03	0.90	0.95
Araneae	Fang	All Araneae,	0.27	1.04	1.09	0.70
Hemiptera	Clavus	All Hemiptera	0.22	0.64	0.54	0.64
Hemiptera	Front tibia	All Hemiptera	0.33	0.98	0.71	0.96
Lepidoptera larvae	Mandible	All Larvae	0.16	0.56	0.56	0.64
Orthoptera	Mandible	All Orthoptera	0.28	1.01	0.72	0.62

[a] Except Carabidae, Scarabaeidae

[b] Faecal samples collected from nocturnal roost sites.

[c] Faecal samples collected from human-imprinted chicks when foraging trials were conducted in the morning, afternoon, or evening and then the faecal matter collected until the following morning.

For those diagnostic fragments from invertebrate types that are often eaten by bobwhite chicks but were not included in this study, the f values of another appropriate diagnostic fragment can be applied to them. In Table 3.5, recovery rates for diagnostic fragments from invertebrate groups not examined in this study are suggested. This was achieved by using, where possible, recovery data from previous studies and by taking into account the nature of its diagnostic fragments i.e. hard or soft. For example, in the case of Aphididae, where the percentage recovery of diagnostic fragments in faecal samples from other bird species is known to be low (Green 1984, Jenni *et al.* 1990), the f values of Lepidoptera larvae were used as this invertebrate type generally had the lowest percentage recovery in this feeding trial.

Table 3.5. Predicted number of diagnostic-fragments that would be recovered per invertebrate ingested from the faeces of 10-day old northern bobwhite chicks. These can be used when calculating (see text) the composition of the diet of wild or human-imprinted northern bobwhite chicks from faecal analysis using the formula described by Green and Tyler (1989).

Invertebrate group	Fragment counted	Calculated from	Recovery per invertebrate (f)			
			Wild chicks	Human -imprinted chicks[b]		
			Roost[a]	Morning	Afternoon	Evening
Aphididae	Tibia	Lepidoptera larvae mandible	0.47	1.69	1.69	1.93
Carabidae Scarabaeidae	Front tibia	Coleoptera tibia	0.52	1.09	1.30	1.25
Diptera	Wing	Lepidoptera larvae mandible	0.16	0.56	0.56	0.64
Formicidae	Femur	Coleoptera femur	0.99	2.46	2.40	2.73
Homoptera	Hind tibia	Hemiptera front tibia	0.33	0.98	0.71	0.96
Isoptera	Mandible	Coleoptera mandible	0.46	1.03	0.90	0.95

[a] Faecal samples collected from nocturnal roost sites.

[b] Faecal samples collected from human-imprinted chicks when foraging trials were conducted in the morning, afternoon, or evening and then the faecal matter collected until the following morning.

4.0 DISCUSSION

This study has demonstrated that if the differential recovery of invertebrate-diagnostic fragments is ignored when conducting faecal analysis, the contribution of some prey items in the diet of bobwhite chicks will be underestimated.

As was also found by Green and Tyler (1989), the recovery proportions of Coleoptera tibia were greater than any other invertebrate-diagnostic fragments examined. The hard chitinous nature of these fragments reduces the potential for them to be broken down in the gizzard and therefore become unrecognizable in the faeces (Jenni *et al.* 1990). While mandibles of Lepidoptera larvae and adult Coleoptera and Orthoptera are also hard, they may be more susceptible to being retained in the gizzard as grit due to their size, shape and texture. As different diagnostic fragments from an individual have different recovery rates, it is essential that the same diagnostic fragment from a particular prey item be counted across all samples when differential recovery is not accounted for. If this is not done, and for example Coleoptera femurs are counted in one sample and Coleoptera tibias in another, differences in differential recovery may mask dietary differences.

As shown in Table 3.3 and Figures 3.2–3.6, faecal samples collected from nocturnal roost sites of wild bobwhite broods probably primarily contain invertebrate prey eaten during the afternoon and evening of the previous day. Because researchers often identify the preferred invertebrates of gamebird chicks by comparing the presence of prey items in faecal samples with their relative abundance in brood-rearing areas (Green 1984, Hill 1985), the results of this study indicate that when diet is determined from samples collected from nocturnal roost sites, it should only be related to the food supply in the habitat patches used by broods during the afternoon and evening. In conjunction with using radio-telemetry to identify brood-foraging sites at specific times, the dietary determination method described here will provide a more accurate examination of invertebrate selection in different habitats.

Even after adjusting samples for differential recovery, soft-bodied prey items that do not have diagnostic fragments may always be underestimated through faecal analysis (Green 1984). For example, Collembola are often found in the crops of grey partridge but are rarely recorded in their faeces (Moreby 1988). Although studies of crops and gizzards from wild and imprinted bobwhite chicks have not identified Collembola in the diet of chicks, low numbers of soft-bodied nymphs of various invertebrates have (Hurst 1972). Therefore, while it must be recognized that faecal analysis may fail to identify some uncommon prey items in the diet, it provides an indirect and non-invasive assessment of the diet of chicks. In imprinted chick foraging studies, using faecal analysis as opposed to gizzard and crop analysis (Palmer *et al.* 2001) makes this research technique more acceptable, both legally and ethically.

The recovery of diagnostic fragments is likely to be influenced by other factors not examined here. Chick age, observer experience, invertebrate size, and diet composition may all influence the proportion of diagnostic fragments recovered in faecal samples. Due to the highly fragmented and digested state of faecal samples, observer experience is more important in accurately determining the diet from faeces than from stomach contents. It is therefore crucial that inexperienced researchers consult with entomologists, use detailed reference collections and published photographic guides to reduce the risk of miss-identifying prey items in samples. Although it is possible that the recovery proportions of diagnostic fragments in bobwhite chick faeces may vary with age, Green (1984) found no differences in the recovery of invertebrates between grey partridge chicks aged 1-10 and 11-20 days old. Although these, and other factors may reduce the accuracy of the adjustment values calculated in this study, it is probable that the use of the adjustment values described here will still provide a more accurate description of the diet of chicks diets than unadjusted faecal assessments.

Correction factors developed for the analysis of faecal samples from one gamebird species have been successfully used on samples from another (Green 1984, Hill 1985). Although it should be recognized that the digestive processes of chicks of one species could vary from those of another, the use of the invertebrate-recovery adjustments developed here may nevertheless be used to increase the accuracy of diet assessments of other gamebird chicks.

Having established this method for examining the diet of chicks from faecal material, this became the primary method by which the diet and invertebrate selection of bobwhite chicks were assessed in the remainder of this study.

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CHAPTER IV

A COMPARATIVE STUDY OF THE DIET AND SELECTION OF INVERTEBRATES BY HUMAN-IMPRINTED AND WILD NORTHERN BOBWHITE CHICKS

SUMMARY

The use of human-imprinted chicks for assessing the foraging value of habitats for gamebird broods has become an increasingly popular technique. While laboratory studies suggest that chick-selection of invertebrate prey is innate, the assumption that prey selection by human-imprinted and wild chicks is similar, remains untested.

Here, in 2003 and 2004, the diet and invertebrate selection of wild and human-imprinted chicks on Tall Timbers Research Station was examined and compared using faecal analysis. Incubator hatched bobwhite chicks were imprinted onto researchers and allowed to forage for 30 minutes at locations where radio-collared wild broods had been located 1-2 hours prior to the trials. To assess invertebrate abundance at these locations, samples were collected using an insect suction sampler.

The Orders Coleoptera, Hemiptera and Hymenoptera accounted for >80% of the invertebrate composition (by number) in the faecal samples of human-imprinted and wild chicks in both years. Greater numbers of Araneae and Orthoptera were found in

the faecal samples of wild chicks than imprinted chicks. Differences between diet compositions did not vary between years. In both chick-types, Chrysomelidae, Curculionidae, and Carabidae were the most numerous groups within the Coleoptera order, while within the order Hemiptera, Heteroptera, Cicadellidae and Aphididae were the most numerous groups. In both years, at order-level, invertebrate prey selection by wild and human-imprinted chicks was non-random. Both chick types, in both years, selected Coleoptera, Hymenoptera and Heteroptera more often relative to their abundance in the field. Wild chicks largely did not select for groups within the orders Hemiptera and Coleoptera, whereas imprinted chicks did.

The results of this study suggest that the use of human-imprinted bobwhite chicks for assessing the foraging value of habitats for wild broods is valid. Therefore, human-imprinted chicks provide researchers with a more biologically relevant technique for measuring the foraging value of habitats than using traditional invertebrate sampling techniques.

1.0 INTRODUCTION

Assessing the foraging value of habitats for insectivorous birds has traditionally been conducted through the measurement of invertebrate prey abundance using standard entomological sampling techniques. These include insect suction samplers, sweep netting and pit fall trapping (Cooper and Whitmore 1990). In studies of gamebird brood foraging habitat quality, invertebrate samples have been collected most commonly using suction samplers (Southwood and Cross 1969, Green 1984, Hill 1985, Burger *et al.* 1993, Hammond 2001) as sweep netting only samples invertebrates on the upper portion of vegetation, while pitfall traps are designed to capture ground dwelling invertebrates (Cooper and Whitmore 1990). Consequently, the composition of invertebrates in samples collected using these techniques is unlikely to represent that present in the foraging-space utilized by gamebird chicks, which for northern bobwhite, *Colinus virginianus*, (henceforth, bobwhite) chicks is from ground litter to a height of 15-20cm (D. Butler, Personal Observation). This space has been termed the 'zone of availability' (Stiven 1961). However, as is also the case with sweep netting, the efficiency of suction sampling can vary between habitat types (Southwood and Henderson 2000). Therefore in gamebirds that utilize many habitat types, such as bobwhite, studying the foraging quality of habitat patches in heterogeneous landscapes is difficult (Palmer *et al.* 2001).

Universal to these techniques is that they do not incorporate a measure of invertebrate-availability to foraging chicks. Consequently they are limited to assessing relative invertebrate abundance within a habitat. Various characteristics of invertebrates, including colouration, activity patterns and palatability, influence which species birds ingest and thereby converting simple invertebrate abundance into availability (Cooper and Whitmore 1990). While the foraging quality of different habitats has often been deduced from linking data from invertebrate samples with that of a previous or simultaneous dietary study (Sotherton 2000), this assumes that availability is constant across habitat types, which, due to environmental factors such as vegetation structure, is unlikely (Hutto 1990).

In order to incorporate a measure of availability, researchers have recorded various indices of habitat quality during and/ or after foraging episodes of captive-reared gamebird chicks. Chicks of bobwhite (Hurst 1970, Jackson *et al.* 1987, Palmer *et al.* 2001, Utz *et al.* 2001) wild turkey, *Meleagris gallopavo*, (Healy 1985), and capercaillie, *Tetrao urogallus*, (Spidsø and Stuen 1988), have been used. To allow the chicks to be used in this manner, they were either imprinted onto bantam chickens (Hurst 1970, Jackson *et al.* 1987) or humans (Healy 1985, Spidsø and Stuen 1988, Palmer *et al.* 2001). While the chicks were foraging, researchers have measured indices of habitat quality by either simply counting the number of successful pecks or by identifying and counting the prey items captured and ingested (Healy 1985, Spidsø and Stuen 1988). These indices, however, are difficult to record in patches of dense vegetation. Therefore, researchers have also examined various indices after the chicks have foraged, including chick-growth rates and the invertebrate-composition in the digestive tracts of the euthanised chicks (Jackson *et al.* 1987, Palmer *et al.* 2001).

One key assumption of using imprinted chicks to assess the foraging quality of habitats is that prey selection by gamebird chicks is innate (Palmer *et al.* 2001). While the results of laboratory feeding studies suggest that captive-reared chicks show a preference for invertebrate groups that are most commonly found in the diet of wild chicks (Vickerman and O'Bryan 1979, Whitmore *et al.* 1986), invertebrate selection by human-imprinted (henceforth, imprinted) and wild chicks foraging in the same habitats has never been studied. The objective of this study was, therefore, to examine and compare invertebrate prey selection by imprinted and wild bobwhite chicks foraging in the same brood-rearing habitats.

2.0 METHODS

2.1 Radio-tracking

In conjunction with a companion study, approximately 100 adult bobwhites were fitted with a 6-g mortality sensing necklace style radio-transmitter (American Wildlife Enterprises, Florida) on Tall Timbers Research Station during spring 2003 and 2004. All birds were captured using baited funnel traps (Stoddard 1931). During the breeding season, April to October, radio-marked birds were located approximately five times per week by homing using a hand-held Yagi antenna. If a bird was located in the same location on ≥ 2 consecutive days, the bird was assumed to be incubating. When the bird was located away from the suspected nesting area, a search for the nest was conducted to confirm that the bird had begun incubation. Incubating birds were monitored daily until hatching. Upon hatching, the radio-tagged birds with chicks (henceforth, radioed-broods) were located 2-3 times daily until 14 days of age.

2.2 Human-imprinting chicks

From the beginning of May, 30-40 bobwhite eggs from wild strain captive birds were hatched each week in an incubator (Georgia Quail Farms, Savannah, Georgia). Each batch of chicks was imprinted onto a human according to Palmer *et al.* (2001) (Plate 4.1). Those chicks that did not imprint, i.e. making lost calls and not brooding, were separated and not used in foraging trials. To facilitate imprinting, chicks were initially housed in a cardboard box approximately 40 × 30 × 30 cm in size and provided commercial gamebird chick food (Purina Mills, Inc., St. Louis, Missouri), and water *ad libitum*. An electric heating pad covering the floor of the box was used as a heat source.

At three days of age, chicks were transferred to brooders (Georgia Quail Farms, Savannah, Georgia), 90cm × 80cm × 24cm in size, with fine wood chips covering the floor and a wire mesh roof. The chicks were housed at a constant temperature (35 °C) using thermostat regulated heat lamps and again provided with commercial gamebird chick food, and water *ad libitum*. From two days of age, chicks were also hand fed crickets (Orthoptera: Gryllidae) to help maintain the chicks bond to the handler and provide experience of handling invertebrate prey (Plate 4.2). The heads of the crickets were removed to prevent the mandibles, a diagnostic fragment of Orthopteran prey, being ingested. When the chicks were between 3-5 days old, they were allowed to forage on a lawn and in weed plots for 1-2 hours each morning and afternoon in order to train them to return to a handler when called and become familiar with foraging in vegetation of various heights.

Plate 4.1. Imprinting northern bobwhite chicks.

Plate 4.2. Feeding crickets to human-imprinted northern bobwhite chicks.

2.3 Imprinted chick-foraging trials

When radioed-broods were between five and 12 days old, two location fixes were obtained in the afternoon on three separate days. Location fixes were at least 1½ hours apart and were taken between 14:30 and 15:15 ("early" locations) and between 16:30 and 17:15 ("late" locations). For each fix, the radioed-brood was initially found using homing and then circled quietly at a distance of approximately 30m until an exact location was obtained. Flagging was used to allow the observer to easily return to the location. Locations were taken at these times of the day because intensive radio-telemetry data suggest that brood foraging activity in the afternoon is at its greatest between 14:00 and 18:00 (D. Butler, Unpublished data).

At each location fix, an imprinted chick foraging trial was conducted. All trials were conducted between 17:00-18:30 on the same afternoon the locations were taken. Trials were only conducted when the vegetation and leaf litter were dry to the touch and the air temperature was approximately 25-30 °C. For each trial, a 'brood' of four chicks were randomly picked from the brooder and placed in a cardboard shoebox with ventilation windows for transportation to the study site. All boxes were lined with clean white paper prior to each trial to allow any faeces produced during carriage to be easily collected. All imprinted chicks used in the trials were between 6-12 days old. To avoid diagnostic fragments of invertebrates ingested during training sessions being present in the faeces collected after a foraging trial, chicks were kept in the brooder for at least 24 hours prior to a trial. No crickets were fed to the chicks on the day of a trial and all food was removed from the brooder two hours prior to a trial.

At the exact point where the radioed-brood had been located, the imprinted chicks were placed on the ground and allowed to forage for 30 minutes wherever they chose. The handler followed the chicks from a distance of approximately 2-5m. If a chick was separated from the 'brood' and began to make 'lost' calls, the handler would call to the chicks to gather them together. Once together, the handler would stop calling to allow them to continue foraging. After 30 minutes foraging, the chicks were collected up and placed back in the shoebox. The box was labeled with the radioed-broods' Id number, the date, time, and location of the trial. These details were also recorded on data sheets.

2.4 Faecal collection

2.4.1 Imprinted chicks

As soon as possible after a trial, each 'brood' was placed in one of eight separate pens constructed within a chick brooder (Plate 3.1). Each pen was 34cm × 23cm × 24cm in size. The pens were constructed from wire mesh and the walls were lined with white paper. The floor of each pen was also constructed of wire mesh, which allowed faeces to fall on to a collecting plate below. The collecting plates were aluminium trays marked with indexed grids to correspond with each pen. A wire mesh roof was placed on each brooder. The chicks were housed at a constant temperature of 35 °C using thermostat regulated heat lamps and small red brooding lights were located over the pens. Chicks were provided with commercial gamebird chick food and water *ad libitum.* Pens were labelled with the same details that were on the carrying boxes.

At 09:00 the following morning, all chicks were removed from the pens and placed back in the brooder with the other imprinted chicks. For each 'brood', all faeces were carefully collected using a pair of tweezers from inside the pen, including in the drinker and food tray, on the collecting plate and in the carrying box. All faeces were placed in a labeled plastic container and stored in a freezer. Used pens and the collecting plate were then cleaned and set up for the next trials.

2.4.2 Wild chicks

To determine what invertebrates the radioed-broods had ingested on the day of the imprinted-chick trials, chick faeces were collected from their nocturnal roost site following the trials. Nocturnal roost sites were found by locating the radioed-broods just prior to sunrise using homing and marking their position with flagging tape at a distance of approximately 5 m in each cardinal direction from the suspected roost site. Once the brood had moved away from the roosting area later that morning, the roost site was identified by the presence of chick-faeces (Plate 4.3). All chick faeces present were placed in a plastic vial using a pair of tweezers, labeled and then stored in a freezer.

Plate 4.3. A nocturnal roost site of a northern bobwhite brood.

2.5 Faecal analysis

Analysis of the wild and imprinted chick faeces was conducted according to Moreby (1988). Faecal material collected from each nocturnal roost site and imprinted-chick 'brood' was prepared and examined separately. In order to remove fine debris and uric acid that can cloud a sample and hamper identifying invertebrate-diagnostic fragments, faecal material were initially washed through a 210 μm sieve and then returned to a plastic vial containing 70% ethyl alcohol until required for analysis.

To determine the invertebrates present in the faecal matter, samples were systematically examined on a Petri dish marked with a 1 × 1 cm grid under a binocular microscope at 25-40× magnification. Invertebrate-diagnostic fragments were identified and counted using, (1) published photographic and illustrative guides (Peterson 1960, 1962, Ralph *et al.* 1985, Moreby 1988); (2) a collection of whole invertebrates; (3) personal communication with S. Moreby, The Game Conservancy Trust, England. To account for differential recovery, the numbers of diagnostic fragments found in each sample were adjusted using the correction factors calculated in Chapter III. The imprinted chick faeces were adjusted using the correction factors calculated for foraging trials conducted in the afternoon (Tables 3.4 and 3.5). For each radioed-brood, the corrected data from the roost site samples as well as the corresponding imprinted-chick faecal samples were pooled before the proportions of each invertebrate group in the diet were calculated.

2.6 Invertebrate sampling

Immediately following the imprinted chick trials, invertebrate samples were collected using a D-Vac® insect suction sampler (D-Vac Company, Ventura, California) (henceforth, D-Vac) at each radioed-brood location. Samples were taken along two 5 m transects centred over the radioed-brood location point. While the first transect was in a random direction, the second was at right angles to the first, thereby forming a cross.

Invertebrate samples were collected by holding the intake cone (opening area = 320 cm^2) of the D-Vac 20cm above the ground and walking at a slow constant pace along each transect (Burger *et al.* 1993, Jackson *et al.* 1987, Manley *et al.* 1994).

Labeled samples were transferred to a freezer for storage. Thawed invertebrates were systematically separated from plant residues and soil particles in each sample. Invertebrates were then identified to an appropriate taxonomic level under a binocular microscope (10-40× magnification). Similarly to the faecal data, the invertebrate samples corresponding to each radioed-brood were pooled before analysis.

2.7 Statistical analysis

Statistical comparisons of the proportional data were carried out using compositional analysis (Aebischer *et al.* 1993). This technique has often been used to analyse bird-dietary data (Brickle and Harper 1999, Moreby and Stoate 2001) especially when comparing the results given by different methods of diet assessment (Poulson and Aebischer 1995, Moreby and Stoate 2000). Since proportional data must sum to 1, the proportions are not linearly independent. To overcome this 'unit-sum constraint' the proportional data are converted to log-ratios. For example, if there are 3 categories describing the diet (sum to 1), the first 2 proportions are divided by the third and then from the resulting ratios, logarithms are taken to normalize their distribution. The log-ratios are independent of the category used as the denominator. To allow log-ratios to be calculated, all zero values are replaced by a very small proportion (0.0001) (Brickle and Harper 1999).

To examine the differences in the composition of invertebrates (by number) in the diet of wild and imprinted chicks, and in the D-Vac samples, the log-ratio differences were calculated for each pair-wise combination. The log-ratio differences were then tested simultaneously by MANOVA to reveal differences in the invertebrate composition between samples. If a significant difference was found, a ranking matrix was produced to determine where the differences lay (Aebischer *et al.* 1993). The differences between samples for all possible pairs of log-ratios were examined using paired *t*-tests. All analyses were conducted using Systat 8.0 (SPSS Inc. 1998).

3.0 RESULTS

In 2003, imprinted chick-foraging trials were conducted at the locations of eight wild broods. For one wild brood, as a consequence of inclement weather, only four foraging trials (over two days) were conducted before the imprinted chicks became too old to use (>12 days). Although after most of the foraging trials all four chicks were successfully gathered up, in nine trials one chick was lost and in two trials, two chicks were lost.

In 2004, imprinted chick foraging trials were conducted at the locations of 10 wild broods. Again due to inclement weather, only four foraging trials (over two days) were conducted on locations of one wild brood. Only one chick was lost during trials in this year.

3.1 Differences in diet composition

3.1.1 Between orders

Due to the limited number of groups that can be statistically compared using compositional analysis, the analysis was initially carried out on seven prey groups, Araneae (includes Opiliones), Homoptera, Heteroptera, Orthoptera, Hymenoptera, Coleoptera, and Others (all remaining prey groups given in Tables 4.1 and 4.2).

No differences in the composition of the diet of imprinted chicks that foraged at the early or late locations were found in 2003 (Wilk's Lambda, $\Lambda = 0.475$, $F_{6,2} = 0.37$, $P = 0.856$) or 2004 ($\Lambda = 0.646$, $F_{6,4} = 0.37$, $P = 0.870$). Data from the different locations were therefore pooled. Because differences between wild and imprinted chick diet composition did not vary significantly between years ($\Lambda = 0.435$, $F_{6,11} = 2.38$, $P =$

0.101), data were therefore also pooled across years. Using the pooled data, significant differences in diet composition between chick types were found ($\Lambda = 0.124$, $F_{6,\,12} = 14.16$, $P = <0.001$) (Table 4.3). Relatively greater proportions of Araneae and Orthoptera and smaller proportions of Hymenoptera and Others were present in the diet of wild chicks than in that of imprinted chicks.

Table 4.1. Mean percentage (by numbers) of invertebrate groups identified in D-Vac samples, and wild and human-imprinted northern bobwhite chick-faecal samples collected on Tall Timbers Research Station, Florida, United States, 2003. D-Vac samples were taken at foraging sites of the wild northern bobwhite broods (n = 8) from which faecal samples were collected. Imprinted chicks foraged at the same locations.

Invertebrate group	Sample type														
	D-Vac[c]					Wild chick faeces[d]					Imprinted chick faeces[c]				
	% in broods[b]	% in samples				% in broods[b]	% in samples				% in broods[b]	% in samples			
		Overall		Within groups			Overall		Within groups			Overall		Within groups	
		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Araneae[a]	100	18.38	2.04			100	12.39	2.08			100	1.83	0.28		
Diptera	100	14.65	2.06			25	0.53	0.28			62.5	2.55	1.65		
Orthoptera	100	12.98	1.43			100	4.55	0.98			87.5	1.84	0.48		
Total Coleoptera	*100*	*7.60*	*0.64*	*100*		*100*	*27.19*	*4.07*	*100*		*100*	*8.63*	*1.55*	*100*	
Carabidae	12.5	0.03	0.03	0.52	0.52	62.5	1.41	0.75	5.15	2.33	62.5	0.53	0.18	4.81	1.57
Staphylinidae	12.5	0.07	0.07	1.28	1.28	50	0.24	0.12	1.04	0.59	12.5	0.18	0.18	2.38	2.38
Elateridae	12.5	0.07	0.07	0.61	0.61	0	0	0	0	0	0	0	0	0	0
Curculionidae	100	1.76	0.39	23.92	5.81	100	4.33	0.80	16.21	2.22	87.5	2.20	0.41	25.83	6.17
Chrysomelidae	100	3.78	0.51	48.49	2.76	100	17.75	3.21	64.37	3.91	100	4.46	1.19	54.56	9.31
Scarabidae	12.5	0.02	0.02	0.32	0.32	25	0.09	0.07	0.47	0.37	25	0.55	0.46	4.64	3.48
Other	100	1.78	0.34	23.77	4.59	100	0.71	0.21	2.48	0.52	87.5	0.46	0.10	4.80	1.00
Larvae	25	0.09	0.06	1.09	0.77	75	2.65	0.69	10.27	2.66	25	0.25	0.17	3.00	2.05
Total Hemiptera	*100*	*26.58*	*2.43*	*100*		*100*	*34.90*	*3.54*	*100*			*10.51*	*1.50*	*100*	
Homoptera	100	20.93	2.53			100	12.72	3.25				3.86	0.80		
Aphididae	87.5	1.14	0.41	4.53	1.97	100	8.28	3.48	21.38	7.24	25	0.33	0.24	2.67	2.08
Cicadellidae	100	15.40	1.87	57.12	3.81	87.5	2.30	0.61	6.50	1.49	87.5	2.01	0.57	22.07	5.84
Cercopidae	100	1.63	0.19	6.18	0.52	75	1.54	0.46	4.89	1.43	75	1.40	0.43	13.35	4.80
Delphacidae	75	1.33	0.61	4.29	1.84	0	0.12	0.12	0.30	0.30	0	0	0	0	0
Other Homoptera	100	1.43	0.34	5.14	1.05	25	0.48	0.33	1.95	1.51	0	0.12	0.12	0.90	0.90
Heteroptera	100	5.65	0.64	22.75	3.91	100	22.18	2.84	64.99	6.17	100	6.65	1.41	61.01	7.62
Total Hymenoptera		*16.83*	*2.03*	*100*			*18.72*	*3.01*	*100*			*72.69*	*1.36*	*100*	
Formicidae	100	13.09	2.00	75.08	4.57	100	18.32	3.03	97.33	1.90	100	72.03	1.55	99.06	0.44
Other Hymenoptera	100	3.74	0.38	24.92	4.57	25	0.39	0.26	2.67	1.90	50	0.66	0.30	0.94	0.44
Total Lepidoptera		*2.60*		*100*					*100*		*62.5*	*1.95*	*0.60*	*100*	
Adults	100	1.73	0.23	68.64	6.35	0	0	0	0	0	0	0	0	0	0
Larvae	100	0.87	0.27	31.36	6.35	62.5	1.72	0.73	100	0	62.5	1.95	0.60	100	0
Others	62.5	0.38	0.07			0	0	0			0	0	0		

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[a] Includes Opilionidae. [b]Percentage occurrence of invertebrate group in each brood. [c]On three separate days, D-Vac sampling and imprinted chick trials were conducted at two locations of each wild brood, therefore resulting in six subsamples of each for each wild brood (only four subsamples taken for one brood). Means were calculated from pooled data for each wild brood. [d]Faeces collected from nocturnal roost sites post imprinted chick foraging trials, therefore three subsamples (only two subsamples taken for one brood). Means were calculated from pooled data for each wild brood.

Table 4.2. Mean percentage (by numbers) of invertebrate groups identified in D-Vac samples, and wild and human-imprinted northern bobwhite chick-faecal samples collected on Tall Timbers Research Station, Florida, United States, 2004. D-Vac samples were taken at foraging sites of the wild northern bobwhite broods (n = 10) from which faecal samples were collected. Imprinted chicks foraged at the same locations.

Invertebrate group	Sample type														
	D-Vac[c]					Wild chick faeces[d]					Imprinted chick faeces[c]				
	% in broods[b]	% in samples				% in broods[b]	% in samples				% in broods[b]	% in samples			
		Overall		Within groups			Overall		Within groups			Overall		Within groups	
		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Araneae[a]	100	10.32	0.92			90	5.07	0.81			60	0,88	0.37		
Diptera	100	20.33	2.09			25	0.13	0.13			60	0.99	0.29		
Orthoptera	100	16.29	1.83			100	4.61	0.82			70	2.70	0.90		
Total Coleoptera	*100*	*4.63*	*0.49*	*100*		*100*	*21.55*	*1.89*	*100*		*100*	*7.89*	*1.96*	*100*	
Carabidae	20	0.05	0.03	0.52	0.52	60	0.34	0.12	1.36	0.42	20	0.30	0.23	2.36	1.59
Staphylinidae	0	0	0	1.28	1.28	10	0.03	0.03	0.18	0.18	0	0	0	0	0
Elateridae	0	0	0	0.61	0.61	0	0	0	0	0	0	0	0	0	0
Curculionidae	90	0.85	0.17	23.92	5.81	100	4.56	1.33	19.39	4.30	60	0.59	0.30	5.54	2.77
Chrysomelidae	100	3.01	0.51	48.49	2.76	100	14.76	0.99	70.67	4.27	100	5.96	1.60	76.10	6.57
Scarabidae	0	0	0	0.32	0.32	25	0.04	0.04	0.15	0.15	30	0.22	0.12	3.12	1.61
Other	90	0.69	0.17	23.77	4.59	100	1.16	0.21	5.21	0.78	80	0.68	0.20	11.11	3.73
Larvae	20	0.03	0.03	1.09	0.77	70	0.67	0.28	3.05	1.19	0	0	0	0	0
Total Hemiptera	*100*	*22.03*	*2.05*	*100*		*100*	*33.48*	*5.25*	*100*		*100*	*13.14*	*3.17*	*100*	
Homoptera	100	18.65	1.59			100	25.19	6.02			100	9.48	3.12		
Aphididae	90	1.97	0.58	4.53	1.97	100	21.33	6.30	53.42	8.51	90	7.59	2.81	43.02	9.52
Cicadellidae	100	15.17	1.35	57.12	3.81	100	3.19	0.48	11.65	2.63	70	1.50	0.40	12.27	4.53
Cercopidae	50	0.72	0.29	6.18	0.52	60	0.61	0.21	2.7	1.03	20	0.39	0.26	3.22	2.61
Delphacidae	75	0.30	0.15	4.29	1.84	0	0	0	0	0	0	0	0	0	0
Other Homoptera	70	0.49	0.16	5.14	1.05	10	0.06	0.06	0.34	0.34	0	0	0	0	0
Heteroptera	100	3.38	0.68	22.75	3.91	100	8.29	1.25	31.9	6.68	100	3.66	0.77	41.49	9.31
Total Hymenoptera	*100*	*23.94*	*2.20*	*100*		*100*	*34.01*	*4.05*	*100*		*100*	*74.22*	*3.61*	*100*	
Formicidae	100	21.37	2.31	75.08	4.57	100	32.47	3.95	95.5	1.30	100	73.37	3.50	98.94	0.87
Other Hymenoptera	100	2.57	0.29	24.92	4.57	70	1.54	0.38	4.5	1.30	20	0.85	0.71	1.06	0.87
Total Lepidoptera	*100*	*1.81*	*0.24*	*100*					*100*		*62.5*	*0.13*	*0.13*	*100*	
Adults	100	1.63	0.25	68.64	6.35	0	0	0	0	0	0	0	0	0	0
Larvae	40	0.18	0.09	31.36	6.35	20	0.21	0.14	100	0	10	0.13	0.13	100	0
Others	50	0.68	0.20			40	0.95	0.45			10	0.06	0.06		

[a] Includes Opilionidae. [b] Percentage occurrence of invertebrate group in each brood. [c] On three separate days, D-Vac sampling and imprinted chick trials were conducted at two locations of each wild brood, therefore resulting in six subsamples for each wild brood (only four subsamples taken for one brood). Means were calculated from pooled data for each wild brood. [d] Feaces collected from nocturnal roost sites post imprinted chick foraging trials, therefore three subsamples (only two subsamples taken for one brood). Means were calculated from pooled data for each wild brood.

Table 4.3. Relative differences in the abundance of invertebrate orders in the diet of wild and human-imprinted bobwhite broods (*n* = 18), Tall Timbers Research Station, Florida, United States, 2003-2004. Groups with low numbered rank were relatively more abundant in the diet of wild chicks than in the diet of human-imprinted chicks and vice versa.

Ranking	Orders
1	Araneae^{a}
2	Orthoptera^{a}
3	Homoptera^{ab}
4	Coleoptera^{a}
5	Heteroptera^{ab}
6	Hymenoptera^{c}
7	Others^{bc}

Different letters between orders indicate significant differences at the 5% level.

3.1.2 Within orders

Hemiptera

Within the order Hempitera, the relative differences in abundance of the groups Aphididae, Cicadellidae and Heteroptera in the diet of wild and imprinted chicks were examined. These groups accounted for over 90% of the Hemipteran component of the diet in both wild and imprinted chicks in 2003 and 2004 (Tables 4.1 and 4.2).

Differences within the Hemipteran component of the diet of wild and imprinted chicks varied significantly between years ($\Lambda = 0.440$, $F_{2,6} = 9.55$, $P = 0.002$). Data for each year were therefore analysed separately. In 2003 significant differences between chick types were found within the Hemiptera component of the diet ($\Lambda = 0.243$, $F_{2,6} = 9.32$, $P = 0.014$). Relative to both Cicadellidae and Heteroptera, wild chicks ate a significantly greater proportion of Aphididae than imprinted chicks (Figure 4.1). No differences were found in 2004 ($\Lambda = 0.727$, $F_{2,8} = 1.50$, $P = 0.279$).

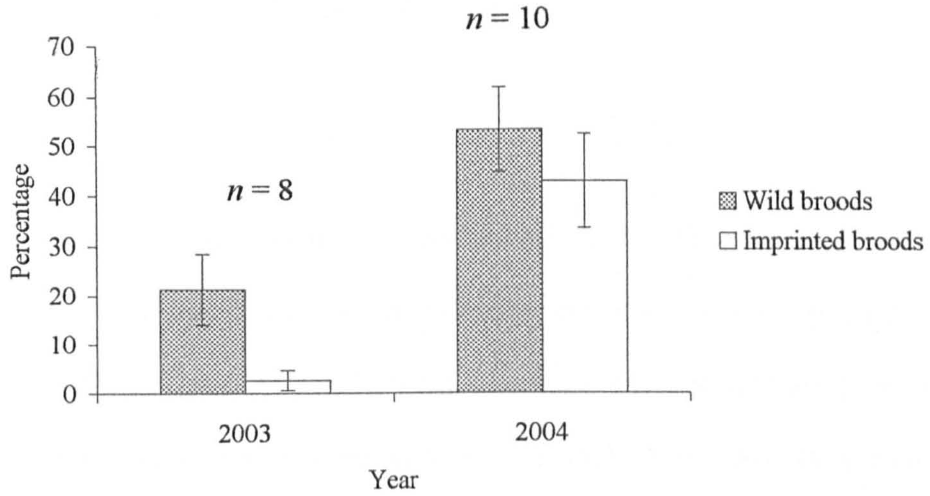

Figure 4.1. Proportion (%) of Aphididae in the Hemipteran component of the diet of wild and human-imprinted northern bobwhite broods foraging on Tall Timbers Research Station, Florida, United States, 2003 and 2004.

Coleoptera

Within the order Coleoptera, the relative differences in abundance of the groups Curculionidae, Chrysomelidae, and Others in the diet of wild and imprinted chicks were examined. Only adults were included. These groups accounted for between 80-95 % of the Coleopteran component of the diet of wild and imprinted chicks (Tables 4.1 and 4.2). Differences within the Coleopteran component of the diet of wild and imprinted chicks did not vary significantly between years ($\Lambda = 0.875$, $F_{2,\,15} = 1.08$, $P = 0.366$). Data were therefore pooled across years. From the pooled data, significant differences between the chick types were found ($\Lambda = 0.636$, $F_{2,\,16} = 4.58$, $P = 0.027$). Relative to Chrysomelidae and Others, the diet of wild chicks contained significantly more Curculionidae than that of imprinted chicks.

3.2 Differences in invertebrate-selection

3.2.1 Between orders

Wild chicks

Differences between the invertebrate composition of the wild chick-diet and that found in the D-Vac samples varied significantly between years ($\Lambda = 0.125$, $F_{6,\ 11} = 12.88$, $P = <0.001$). Therefore data for each year were analysed separately. Invertebrate selection by wild chicks was non-random in both 2003 ($\Lambda = 0.007$, $F_{6,\ 2} = 46.54$, $P = 0.021$) and 2004 ($\Lambda = 0.016$, $F_{6,\ 4} = 41.31$, $P = 0.001$). In both years, wild chicks selected for Heteroptera and Coleoptera relatively more than any other groups (Table 4.4).

Table 4.4. Abundance of invertebrate groups in the diet of wild and human-imprinted northern bobwhite chicks relative to their abundance in D-Vac samples, Tall Timbers Research Station, Florida, United States, 2003-2004. Groups are ranked in order of their relative abundance in the faecal samples in each pair.

Rank	Year			
	2003		2004	
	Wild:D-Vac	Imprinted:D-Vac	Wild:D-Vac	Imprinted:D-Vac
1	Heteroptera^{a}	Hymenoptera^{a}	Coleoptera^{a}	Hymenoptera^{a}
2	Coleoptera^{a}	Coleoptera^{b}	Heteroptera^{b}	Coleoptera^{ab}
3	Hymenoptera^{b}	Heteroptera^{bc}	Hymenoptera^{c}	Heteroptera^{b}
4	Araneae^{bc}	Homoptera^{bc}	Homoptera^{cd}	Homoptera^{bc}
5	Homoptera^{bc}	Araneae^{d}	Orthoptera^{d}	Orthoptera^{cd}
6	Orthoptera^{c}	Other^{cd}	Araneae^{cd}	Araneae^{d}
7	Other^{c}	Orthoptera^{e}	Other^{cd}	Other^{d}

Within pairs, different letters between orders indicate significant differences at the 5% level.

Imprinted chicks

Differences between the invertebrate composition in the imprinted chick-diet and that found in the D-Vac samples varied significantly between years ($\Lambda = 0.243$, $F_{6,\ 11} =$

5.72, P = 0.006). Again, data for each year were therefore analysed separately. Invertebrate selection by imprinted chicks was non-random in both 2003 and 2004 (2003: $\Lambda = 0.01$, $F_{6,2} = 40.23$, $P = 0.024$, 2004: $\Lambda = 0.05$, $F_{6,4} = 12.28$, $P = 0.015$). In both 2003 and 2004, while Hymenoptera and Coleoptera were the orders most heavily selected by imprinted chicks, while Orthoptera, Araneae and Others were selected much less often than expected from their abundance in the field (Table 4.4).

3.2.2 Within order - Hemiptera

Wild chicks

Within the Hemiptera group, differences between the invertebrate composition in the wild chick-diet and that found in the D-Vac samples varied significantly between years ($\Lambda = 0.318$, $F_{2,15} = 16.11$, $P = <0.001$). Selection of the three Hemiptera groups by imprinted chicks was random in 2003 ($\Lambda = 0.387$, $F_{2,6} = 4.75$, $P = 0.058$) but not in 2004 ($\Lambda = 0.100$, $F_{2,8} = 36.13$, $P = <0.001$) (Table 4.5). In 2004, wild chicks selected significantly less Cicadellidae relative to Aphididae and Heteroptera.

Table 4.5. Abundance of Hemipteran groups in the diet of wild and human-imprinted northern bobwhite chicks relative to their abundance in D-Vac samples, Tall Timbers Research Station, Florida, United States, 2003-2004. Groups are ranked in order of their relative abundance in the faecal samples in each pair.

Rank	Year			
	2003		2004	
	Wild:D-Vac	Imprinted:D-Vac	Wild:D-Vac	Imprinted:D-Vac
1	NS	Heteroptera^a	Aphididae^a	Aphididae^a
2		Cicadellidae^b	Heteroptera^a	Heteroptera^a
3		Aphididae^b	Cicadellidae^b	Cicadellidae^b

Within pairs, different letters between orders indicate significant differences at the 5% level.

Imprinted chicks

Differences between the Hemiptera composition in the imprinted chick-diet and that found in the D-Vac samples varied significantly between years ($\Lambda = 0.513$, $F_{2, 15} = 7.13$, $P = 0.007$). Selection by imprinted chicks was non-random in both 2003 and 2004 (2003: $\Lambda = 0.305$, $F_{2, 6} = 6.83$, $P = 0.028$, 2004: $\Lambda = 0.377$, $F_{2, 8} = 6.62$, $P = 0.020$) (Table 4.5). In 2003 Heteroptera were selected significantly more relative to Cicadellidae and Aphididae. In 2004, as was the case for wild chicks, Aphidiadae and Heteroptera were selected significantly more than Cicadellidae relative to their abundance in the D-Vac samples.

3.2.3 Within order - Coleoptera

Wild chicks

Within the Coleoptera group, differences between the invertebrate composition in the wild chick-diet and that found in the D-Vac samples did not vary significantly between years ($\Lambda = 0.817$, $F_{2, 15} = 1.69$, $P = 0.219$). From the pooled data, selection of the three Coleoptera groups by wild chicks was random ($\Lambda = 0.857$, $F_{2, 16} = 1.34$, $P = 0.291$).

Imprinted chicks

Within the Coleoptera group, differences between the invertebrate composition in the imprinted chick-diet and that found in the D-Vac samples varied significantly between years ($\Lambda = 0.619$, $F_{2, 15} = 4.63$, $P = 0.027$). Selection was non-random in both 2003 and 2004 (2003: $\Lambda = 0.288$, $F_{2, 15} = 7.40$, $P = 0.024$, 2004: $\Lambda = 0.411$, $F_{2, 8} = 5.72$,

$P = 0.029$) (Table 4.6). While in 2003 Curculionidae were selected significantly more than Chrysomelidae and Other, in 2004 the reverse was the case.

Table 4.6. Abundance of Coleopteran groups in the diet of wild and human-imprinted northern bobwhite chicks relative to their abundance in D-Vac samples, Tall Timbers Research Station, Florida, United States, 2003-2004. Groups are ranked in order of their relative abundance in the faecal samples in each pair.

Rank	Year			
	2003		2004	
	Wild:D-Vac	Imprinted:D-Vac	Wild:D-Vac	Imprinted:D-Vac
1	NS	Curculionidae[a]	NS	Chrysomelidae[a]
2		Chrysomelidae[b]		Other[a]
3		Other[b]		Curculionidae[b]

Within pairs, different letters between orders indicate significant differences at the 5% level.

4.0 DISCUSSION

In this study, the imprinting method described by Palmer *et al.* (2001), was used successfully to imprint groups of 30-40 bobwhite chicks each week during the breeding season. In the 104 foraging trials conducted, only 14 chicks were lost. In my opinion, the higher loss rate experienced in 2003 was due to giving the chicks insufficient foraging practice when they were between 3 and 5 days old.

At the level of order, invertebrate selection by wild and imprinted bobwhite chicks was broadly similar. Both chick types, in both years, selected for Coleoptera, Heteroptera and Hymenoptera and avoided Other and Orthoptera. These selection rankings are similar to those reported by Hurst (1970) where both imprinted (foraging with a bantam hen) and wild chicks foraging in old-field habitat in Mississippi showed preferences for Coleoptera and Heteroptera and avoided Orthoptera and Diptera. In another study in Mississippi 20 years later, Jackson *et al.* (1987) also reported Coleoptera and Heteroptera being the most selected prey items of imprinted chicks foraging with a bantam hen. However, unlike this study, Hymenoptera were not an important item for imprinted chicks in either of these earlier studies (Hurst 1970, Jackson *et al.* 1987). In this study, the Hymenopteran component of the diet of both wild and imprinted chicks comprised primarily (>90%) of Formicidae. Although these Formicidae were not identified to species, Hurst (1970) reported that most of the Formicidae eaten by imprinted chicks foraging in a similar habitat were fire ants, *Solenopis invicta*. These non-native ants often sting bobwhite chicks on their feet and eyes causing inflammation and irritation (Pedersen *et al.* 1996). In a field experiment by Pedersen *et al.* (1996), captive-reared chicks were often observed pecking the ants from their bodies to avoid being stung. This behaviour was also often seen during the foraging trials in this study. If the imprinted chicks ingested the ants they had picked from themselves this would have artificially increased the proportion of ants in their diet. If wild chicks, on the other hand, learn to either avoid contact with fire ants or not ingest them after picking them from their bodies, this could explain why a much higher proportion of Formicidae were found in the diet of imprinted chicks than wild chicks. Although wild chicks may not choose to eat fire ants, other Formicidae still formed a high proportion of the diet. Other gamebird chicks around the world have also been found to consume high numbers of Formicidae, particularly during the first two weeks of life (Vickerman and O'Bryan 1979, Serre and Birkan 1985, Drut *et al.* 1994, Moreby *et al.* 1999).

As found in previous studies, both imprinted and wild bobwhite chicks ate far less Orthoptera than were present in the brood foraging areas (Hurst 1970, Jackson *et al.* 1987). Rather than Orthoptera being avoided by chicks, it is more likely that the size (Hurst 1970) and activity patterns (Parker 1982, Willot 1997) of these invertebrates make them unavailable to foraging chicks. Consequently, land managers should be careful not to perceive habitat patches with high numbers of Orthoptera as valuable foraging areas for bobwhite chicks.

In this study, wild bobwhite chicks did not generally select prey within the orders Hemiptera and Coleoptera, whereas the imprinted chicks did. Non-selection within orders by wild chicks may indicate a low availability of prey items. Because bobwhite chicks have a high requirement for invertebrates (Palmer 1995), it is probable that in habitat patches where availability levels are below those required by wild chicks, they cannot afford nutritionally to select below the taxonomic level of order. By contrast, the imprinted chicks could afford to be selective within these orders because they were being fed a high protein diet in their pens and were therefore under no pressure to satisfy their daily food requirement with invertebrates. For this hypothesis to be correct, chicks must, at least partially, select invertebrates according to their nutritional value. In a self-selection experiment, Borg and Toft (2000) reported that captive-reared grey partridge chicks could obtain the most nutritional diet available to them through prey selection. Although not conclusive, the results of this study also suggest a relationship between invertebrate selection by chicks and nutritional value of prey. In a study by Robel *et al.* (1995) the calorific values of different invertebrates were calculated. Within the order Hemiptera, the energy content of Cicadellidae (5685 cal/g) (dry mass) was lower than Miridae (6031 cal/g), a commonly eaten Heteropteran group. Interestingly, imprinted chicks in both years of this study, and wild chicks in the second year, preferred the group Heteroptera over Cicadellidae. It may therefore be the case that imprinted chicks consume the most nutritional diet within a habitat patch.

In feeding trials, bobwhite chicks have demonstrated an innate preference for prey items coloured green, green-yellow, and brown and an avoidance of red (Mastrota and Mench 1995). This instinctive behaviour is thought to allow chicks to avoid toxic or unpalatable food items (Mastrota and Mench 1995). Conforming to this theory, no aposematically coloured prey were found in the faeces of wild or imprinted chicks in this study despite being present in some D-Vac samples.

Although Potts (1986) observed female grey partridges selecting sawfly larvae for their chicks, the practice of adult gamebirds feeding their young is thought to be rare (Brennan 1999). It is, however, more likely that adults guide their broods to invertebrate prey using vocal communication. Communication within foraging bobwhite broods is frequent (Brennan 1999) and in wild turkeys, hens have been observed attracting their chicks to more favourable prey items (Kimmel and Healy 1987). Although this behaviour is thought to contribute little to invertebrate selection (Kimmel and Healy 1987), it may have a greater influence on the foraging paths taken by chicks. It is unknown whether imprinted chicks would select a similar foraging path to that of wild chicks but, as also observed by Palmer *et al.* (2001), imprinted chicks in this study mimicked the foraging behaviour of wild chicks by spreading out, up to 2m apart, and slowly moving through the vegetation in search of food (Stoddard 1931). Foraging path selection by wild and imprinted bobwhite chicks deserves further study.

4.1 Study design

In studies that have used imprinted chicks to assess invertebrate availability within different habitats, the number of chicks required for the trials could be foreseen and planned for. However in this study, the number of imprinted chicks required each week was unknown due to the unpredictability of nest hatches on the study site. Furthermore, as chicks were not euthanised after the foraging trials, the number hatched was kept to a minimum due to the facilities and manpower required to house them post trials. Consequently, in order for sufficient numbers of imprinted chicks to be available for trials when wild broods were present on the study site, some imprinted chicks were used in more than one foraging trial. In the studies by Healy (1985) and Spidsø and Stuen (1988) imprinted chicks were also used in more than once. While individual chicks were used more than once, the same 'brood' was unlikely to have been used twice as chicks were randomly selected for each trial. By reusing chicks it was assumed that they did not alter their invertebrate selection by experiencing a foraging trial or trials. Because all chicks were given foraging-practice sessions totalling approximately 12 hours before being used in trials, it is likely that the experience of foraging for a further 30 minutes or 1 hour would have had minimal effect on chick-invertebrate selection. It was also assumed that invertebrate-diagnostic fragments ingested in one trial were digested or expelled from the chicks' digestive tract prior to being used in a subsequent trial. The minimum time lapsed between two trials in which the same chick was used would have been 24 hours. As found in Chapter III, no invertebrate-diagnostic fragments were found in faeces collected 24 hours after bobwhite chicks were fed various invertebrates, so this assumption would appear to be valid.

Because of the difficulty in matching hatch dates, the age of the wild and imprinted chicks usually differed, usually by 2-3 days. However, because chick-age was not found to affect invertebrate composition in the diet of wild chicks, (Chapter V), it was assumed that any invertebrate selection differences found between the two types of chicks were not due to this small difference in age.

This study describes a method for using non-invasive faecal analysis to examine the diet of imprinted chicks. Consequently, the use of this method rather than crop and gizzard analysis may make the use of imprinted chicks a more ethically acceptable and legally viable research tool. Although, Utz *et al.* (2001) reported that these techniques resulted in different estimates of invertebrate composition, it is probable that their result was due to not accounting for differential digestion. As demonstrated in Chapter III, differences in the digestion of diagnostic fragments can considerably influence the number recovered in faecal samples. Therefore, any future imprinted chick studies that use faecal analysis should account for differential digestion by using the correction factors developed in Chapter III.

In addition to identifying the invertebrates most selected by bobwhite chicks, this study has shown that human-imprinted chicks foraging in a habitat will consume similar invertebrate items as wild chicks. Therefore, human-imprinted chicks offer researchers an improved technique for assessing invertebrate-availability and will consequently aid in the formulation and appraisal of management prescriptions to ensure the provision of quality foraging habitat for bobwhite broods.

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CHAPTER V

THE INVERTEBRATE COMPOSITION IN THE DIET OF NORTHERN BOBWHITE CHICKS IN THE SOUTHEASTERN UNITED STATES: IMPLICATIONS FOR GROWTH AND SURVIVAL

SUMMARY

Between 2002 and 2004, the invertebrate diet of northern bobwhite chicks was examined on farmland in central Georgia and two plantations in northern Florida and southern Georgia in the United States. Broods from which faecal samples were collected were also captured at approximately 10 days old to provide data on growth rates and survival.

Each year, on all sites, Coleoptera, Hemiptera and Hymenoptera collectively formed over 70% of the invertebrate diet of chicks. However, at the level of order, invertebrate composition in the diet of chicks varied between the three study sites. While the proportion of Others, predominantly Lepidopotera larvae and Diptera, was significantly higher in the diet of chicks on Farmland than on both plantations, more Hymenoptera were eaten by chicks on the plantations. Composition within the orders Hemiptera and Coleoptera also differed between sites. Age had no effect on the composition of invertebrates in the diet of chicks.

Although the mean growth rate of chicks within broods did not vary between sites, the proportion of the group Others in the diet had a significant negative effect on the mean daily chick growth rate of broods. In addition, the variation in the growth rates of chicks within broods was positively related to the proportion of Others and Homoptera in the diet of broods. Percentage of chicks within broods surviving to 10 days was not affected by the composition of invertebrates in the diet. The implications of these findings for bobwhite management are discussed.

1.0 INTRODUCTION

Providing a rich source of protein, invertebrates form over 80% of the diet of northern bobwhite, *Colinus virginianus*, (henceforth, bobwhite) chicks during the first two weeks life (Stoddard 1931). After this time, the proportion of invertebrates in the diet gradually decreases and seeds and other vegetative matter become the primary food source (Stoddard 1931). The daily number of individual prey items required by gamebird chicks depends upon the size and nutritional value of the invertebrates within the diet (Southwood and Cross 2002). In grey partridge, *Perdix perdix*, for example, Southwood and Cross (2002) reported that a nine-day-old grey partridge chick feeding entirely on Heteroptera requires 4500 fewer items than one eating only Coleoptera. For bobwhite chicks to attain normal growth rates, feeding trials conducted by Palmer (1995) suggest that a 7-10 day old chick requires approximately 6g of invertebrates daily. In addition to protein, invertebrates also provide chicks with essential amino acids. The amino acids methionine and lysine have been identified as particularly important in feather development of poultry and gamebird chicks (Almquist 1952, Scott *et al.* 1963, Potts 1986). Consequently, gamebird chicks that are unable to eat sufficient quantities of invertebrates also suffer from poorer feather development as well as reduced growth rates (Dahlgren 1990, Liukkonen-Anttila *et al.* 2002, Southwood and Cross 2002).

In the wild, the effects of an invertebrate-poor diet increase the vulnerability of grey partridge chicks to chilling and predation (Potts 1986). In field studies in Great Britain, the proportion of preferred invertebrates in the diet of grey partridge chicks was found to be crucial in determining survival rates, which, in turn, affect population levels

(Potts 1986). Despite these findings, the survival of wild bobwhite chicks, especially in relation to diet, is one of the least studied aspects of the species biology (Roseberry and Klimstra 1984, Jackson *et al.* 1987). Although the importance of invertebrates in the diet of bobwhite chicks was first reported in the 1930's, few studies have examined the diet of wild chicks since (Stoddard 1931, Hurst 1972). Furthermore, because no studies have related invertebrate composition in the diet to survival or any other measure of fitness, the dietary importance of different prey items is unknown. As Gullion (1966) commented, 'the presence of certain food items in the digestive system, even in abundance or with considerable frequency over a span of a year or two, is not evidence that the food items concerned were nutritious or even desirable'.

Since the middle of the last century, there has been a widespread decline in the numbers of bobwhite on agricultural landscapes across its geographical range (Church *et al.* 1993). Bobwhite biologists have often hypothesized that modern farming practices, particularly the greatly increased use of pesticides, have been the major contributing factors (Brennan 1991). Echoing the grey partridge situation in Great Britain, it is thought that the intensification of farming in the United States has reduced the availability of chick-invertebrate prey in brood-rearing areas and, as a consequence, caused chick survival rates to decline due to their inability to obtain sufficient quantities of key invertebrates (Stromborg 1982, Brennan 1991). In contrast to the declines experienced on agricultural landscapes, bobwhite populations on the highly managed shooting plantations in southern Georgia and northern Florida have remained relatively stable over the same time period (Brennan *et al.* 2000). Using an array of management prescriptions, plantation managers create and maintain a mosaic of various habitats required by bobwhite during their different life stages (Stoddard 1931). Managers are well aware of the importance of providing quality foraging habitats for bobwhite broods and therefore often use prescribed fire and disking to encourage the growth of succulent forbacious plants that harbour high densities of invertebrates.

Because significantly more brood-habitat management is conducted on plantations than on farmland in the southeastern United States, and, bobwhite-population levels are more stable on these highly managed areas, the aims of this study were to 1) examine and compare the invertebrate composition in the diet of bobwhite chicks on plantations and farmland in the southeastern United States, and 2) examine the effect of the invertebrate composition in the diet of chicks on growth and survival.

2.0 METHODS

In conjunction with a companion study, 100 adult bobwhites were captured and fitted with a 6-g mortality sensing necklace style radio-transmitter (American Wildlife Enterprises, Florida) on Tall Timbers Research Station (TTRS) in northern Florida and Pebble Hill Plantation (PH) in southern Georgia, United States, during late winter and spring 2002-2004. During spring 2002 and 2003 adult birds were also radio-collared on farmland in central Georgia. A detailed description of the study sites is given in Chapter II. All birds were captured using baited funnel traps (Stoddard 1931). During the breeding season, (April to October), birds were located approximately five times per week by homing using a hand-held Yagi antenna. If a bird was located in the same location on ≥ 2 consecutive days, the bird was assumed to be incubating. When the bird was located away from the suspected nesting area, a search for the nest was conducted to confirm that the bird had begun incubation and determine clutch size. Incubating birds were located every day. Upon hatching, the nest was visited within three hours after the brood had departed. The initial brood size was determined from the presence of eggshells, unhatched eggs and dead chicks (Park *et al.* 2001). Diurnal locations of broods were then taken 2-3 times daily until 14 days of age. In addition, the nocturnal roost sites (henceforth roost sites) of broods were also located. Roost sites were located either at dusk or dawn, depending on weather conditions, and marked with flagging tape in each cardinal direction at a distance of approximately 5 m from the radioed-brood. Once the brood had moved away from the roosting area, the roost site was located and all chick-faecal matter was placed in a labelled plastic container using a pair of tweezers and then frozen. Adult faecal matter was not collected and was easily distinguished from that of the chicks as the droppings were much larger and were usually located >50 cm from the centre of the roost site.

2.1 Faecal analysis

Analysis of faecal samples was conducted according to Moreby (1988). Faecal material collected from each nocturnal roost site was examined separately. In order to remove fine debris and uric acid that can cloud a sample and hamper identifying invertebrate-diagnostic fragments, faeces were initially washed through a 210 μm sieve and then returned to a plastic vial containing 70% ethyl alcohol until required for analysis.

To determine the invertebrates present in the faecal matter, samples were systematically examined on a Petri dish marked with a 1 × 1 cm grid under a binocular microscope at 25-40× magnification. Invertebrate-diagnostic fragments were identified and counted using, (1) published photographic and illustrative guides (Peterson 1960, 1962, Ralph *et al.* 1985, Moreby 1988); (2) a collection of whole invertebrates; (3) personal communication with S. Moreby, The Game Conservancy Trust, England. To account for differential recovery of diagnostic fragments from different invertebrates within a faecal sample, the proportion of each prey type in faecal samples was calculated using the formula described by Green and Tyler (1989) that incorporates the correction factors produced in Chapter III (Tables 3.4 – 3.5). For each radioed-brood, the corrected data were pooled before the proportions of each invertebrate group in the diet were calculated.

2.2 Chick-capture and measurement

At approximately 10 days of age (range, 8-12 days), radioed-broods were captured at dawn by encircling the roosting brood with a small fence as described by Smith *et al.* (2003). All vegetation was then carefully removed from inside the enclosure to ensure that all the chicks in the brood were captured. While removing the vegetation, the adult bird would flush out of the enclosure but remain close to the perimeter calling to the chicks. The exact age at which broods were captured varied due to weather conditions and available manpower. All captured chicks were weighed to the nearest 0.25g using a Pesola® spring balance and any physical abnormalities noted. As the chicks from different bobwhite broods can become mixed and therefore create a 'mixed brood' (Faircloth *et al.* 2005), each captured brood was classified according to the extent to which brood mixing was thought to have occurred. Three categories were used; Not Suspected, Moderately Suspected and Highly Suspected (Hammond 2001). The criteria on which broods were classified were number of chicks caught, flight ability, and feather growth of chicks. A brood was classified as Highly Suspected if the number of chicks captured exceeded the initial brood size at hatch. If chicks within a brood aged ≤12 days old were able to easily fly over the fence during capture, the brood was classified as Moderately Suspected as bobwhite chicks are unable to fly until approximately 14 days of age (Brennan 1999). Broods were also classified as Moderately Suspected if primaries had not begun to emerge on one or more chicks in broods aged ≥8 days old (Brennan 1999). All other broods were classified as Not Suspected. After all the chicks were measured, they were released in close proximity to the adult. All chick-faecal matter was collected using tweezers and placed in a labelled plastic container and frozen.

2.3 Statistical analysis

2.3.1 Diet composition

Diet composition of chicks was examined using compositional analysis (Aebischer *et al.* 1993). Since proportional data must sum to 1, the proportions are not linearly independent. To overcome this 'unit-sum constraint' the proportional data are converted to log-ratios. For example, if there are 3 categories describing the diet (sum to 1), the first 2 proportions are divided by the third and then from the resulting ratios, logarithms are taken to normalize their distribution. The log-ratios are independent of the category used as the denominator. To allow log-ratios to be calculated, all zero values are replaced by a very small proportion (0.0001) (Brickle and Harper 1999). Comparisons between the relative abundance of six invertebrate Orders; Araneae, Hemiptera, Orthoptera, Hymenoptera, Coleoptera and Other (all other groups in Tables 5.1-5.3), and within the orders Hemiptera and Coleoptera were made in relation to chick age, study site and year. Within orders the three most abundant taxonomic or biological groups were compared, Hemiptera (Aphididae, Heteroptera and other Homoptera) and Coleoptera (Chrysomelidae adults and larvae, Curculionidae and other Coleoptera).

2.3.2 Growth rates

The mean daily growth rate of each chick in a brood, expressed in grams/ day, was calculated for the interval between hatch and capture according to Bradbury *et al.* (2003).

Growth Rate = (mass at capture – mass at hatch)/ interval from hatch to capture

As broods were not captured at hatch, it was assumed that chick weight was 6 g at hatch (Brennan 1999). For analysis, a mean daily growth rate was then calculated for each brood. Chick growth rate data were only used from broods classified as 'Not Suspected' of brood mixing.

2.3.3 Chick survival

Including only those broods that were 'Not Suspected' of being a mixed brood, the Daily Survival Rate (*DSR*) of chicks within each brood with ≥ 1 chick at capture was calculated using the Mayfield method (Mayfield 1961, 1975). *DSR* for chicks within each individual brood was estimated as:

$DSR = 1 - (\Delta \text{ brood size/ exposure days})$,

where Δ brood size is the change in brood size during the observation interval between hatch and capture. Exposure days were calculated by multiplying the number of chicks in the brood by the number of days between hatch and capture. To calculate chick exposure days when chicks were lost from a brood, all losses were assumed to have occurred at the midpoint between hatch and capture (Mayfield's midpoint assumption;

Johnson 1979) (Flint *et al.* 1995, DeMaso *et al.* 1997). Therefore a loss would have been assigned exposure days equal to half of the observation interval. For example, if a nest hatched 11 eggs and 8 chicks were caught 10 days later, the exposure days would be $(11 \times 5) + (8 \times 5) = 95$ days. To estimate chick survival to 10 days, the *DSR* for each brood was raised by a power of 10 (Johnson 1979). All survival estimates were multiplied by 100 to determine percentage survival. To normalise distribution, data were *arcsine* transformed prior to analysis.

2.3.4 Influence of diet on growth rates and survival

The invertebrate composition in the diet of each brood that provided data on chick survival and / or growth rates was determined by using only faecal samples collected from hatching to capture. To determine which dietary groups were responsible for variations in chick survival and growth rates, the data were initially analysed using forward stepwise multiple regression analysis. The arcsine transformed proportions of seven dietary groups were included in the starting models: Aranaeae, Coleoptera, Homoptera, Heteroptera, Hymenoptera, Orthoptera, and Others (all other groups in Tables 5.1-5.3). In separate regression analyses the relationships between the collective proportion of the two most selected invertebrate groups in the diet and chick survival and growth were also investigated. The two most selected invertebrate groups of wild bobwhite chicks, Heteroptera and Coleoptera, were identified in Chapter IV (Table 4.4). To account for the effects of year and site, a site-year factor was included in all models.

3.0 RESULTS

3.1 Diet composition

Between 2002-4, a total of 302 faecal samples from 70 broods and 177 samples from 29 broods were collected on TTRS and PH, respectively. In 2002-3, 89 faecal samples were collected from 19 broods on Farmland. The invertebrate composition in the diet of chicks on each study site is described in Tables 5.1– 5.2.

3.2 Chick age

Using data collected between 2002-2004, the invertebrate composition in the diet of chicks aged 1-7 days and 8-14 days was compared on TTRS (n = 23 broods), PH (n = 11 broods) and Farmland (n = 7 broods). Only broods that were 'Not Suspected' of being a mixed brood at capture and also supplied faecal matter for both age categories were included in the analysis. For each brood, the corrected data from samples within each age category were pooled before the proportions of each invertebrate group were calculated. The log-ratio differences between the two age groups were then calculated for each pair-wise combination and tested simultaneously by MANOVA for overall departure from randomness.

At the level of order, the invertebrate composition within the diet of chicks aged 1-7 days and 8-14 days did not vary significantly on TTRS (Wilk's Lambda, $\Lambda = 0.743$, $F_{5,18} = 1.245$, $P = 0.330$), PH ($\Lambda = 0.269$, $F_{5,6} = 3.253$, $P = 0.092$) or Farmland ($\Lambda = 0.216$, $F_{5,2} = 1.448$, $P = 0.456$) (Figure 5.1). Chick-age also had no effect on the composition of invertebrates within the orders Coleoptera (TTRS: $\Lambda = 0.964$, $F_{2,21} = 0.396$, $P = 0.678$, PH: $\Lambda = 0.706$, $F_{2,9} = 1.873$, $P = 0.209$, Farmland: $\Lambda = 0.863$, $F_{2,5} =$

Table 5.1. Mean percentage (by numbers) of invertebrate groups in the diet of northern bobwhite chicks on Tall Timbers Research Station in northern Florida, United States, 2002-2004. Faecal samples were collected from nocturnal roost sites of broods with a radio-collared adult until 14 days old.

	Year														
	2002[a]					2003[b]					2004[c]				
Invertebrate Group	% occurrence in broods	% in samples				% occurrence in broods	% in samples				% occurrence in broods	% in samples			
		Overall		Within groups			Overall		Within groups			Overall		Within groups	
		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Araneae	68.6	3.42	0.63			83.3	8.29	1.37			95.7	5.05	0.69		
Diptera[d]	17.1	0.43	0.21			41.7	0.30	0.12			30.4	0.33	0.16		
Isoptera	0	0	0			0	0	0			21.7	0.07	0.04		
Lepidoptera – larvae	51.4	3.30	1.32			66.7	2.42	1.07			43.5	0.43	0.13		
Neuroptera – larvae	5.7	0.06	0.04			8.3	0.67	0.67			30.4	0.29	0.11		
Orthoptera	91.4	7.04	1.42			100	4.04	0.72			87.0	6.11	1.73		
Total Coleoptera[d]	*100*	*23.16*	*2.71*	*100*		*100*	*24.26*	*3.52*	*100*		*100*	*34.87*	*4.62*	*100*	
Cantharidae	8.6	0.02	0.01	0.08	0.05	58.3	0.49	0.19	2.05	0.73	60.9	0.45	0.14	2.06	0.69
Carabidae – adults	54.3	1.26	0.37	5.04	1.31	58.3	0.80	0.37	3.58	1.51	56.5	0.21	0.06	0.82	0.22
Carabidae – larvae	2.9	0.04	0.04	0.19	0.19	0	0	0	0	0	13.0	0.08	0.08	0.27	0.16
Chrysomelidae – adults	97.1	10.85	1.82	42.10	3.63	100	14.78	3.16	55.79	5.24	100	29.46	4.61	80.61	2.67
Chrysomelidae – larvae	48.6	1.55	0.52	7.99	2.34	66.7	1.76	1.07	7.02	4.02	39.1	0.81	0.53	1.88	0.97
Curculionidae	94.3	5.00	0.78	27.33	3.08	100	4.59	0.72	20.94	2.89	91.3	2.44	0.46	8.84	1.77
Elateridae	8.6	0.01	0.01	0.13	0.08	8.3	0.02	0.02	0.14	0.14	8.7	0.02	0.01	0.11	0.08
Scarabidae	0	0	0	0	0	50	0.15	0.07	0.67	0.35	34.8	0.21	0.13	0.72	0.37
Staphylinidae	28.6	0.40	0.29	1.51	0.85	33.3	0.25	0.16	3.85	3.52	21.7	0.04	0.02	0.15	0.06
Other – adults	85.7	3.81	1.22	14.57	3.17	91.7	1.36	0.24	5.77	1.18	82.6	0.99	0.18	3.96	0.71
Others – larvae	14.3	0.22	0.14	1.09	0.56	8.3	0.07	0.07	0.20	0.20	30.4	0.18	0.06	0.57	0.19
Total Hemiptera	*100*	*37.24*	*4.08*	*100*		*100*	*40.57*	*5.97*	*100*		*100*	*30.27*	*3.78*	*100*	
Homoptera	88.6	27.04	4.72			100	23.42	7.14			95.7	23.54	4.10		
Aphididae	80	22.72	4.96	45.69	6.51	83.3	18.44	7.45	33.63	9.14	90.9	19.25	4.34	51.79	6.13
Cicadellidae	74.3	2.90	0.84	10.49	2.61	100	3.04	0.48	9.80	2.33	90.9	2.79	0.41	12.26	2.18
Cercopidae	54.3	1.42	0.62	4.65	1.41	75	1.80	0.61	6.26	2.45	82.6	1.29	0.32	6.36	1.73
Delphacidae	0	0	0	0	0	8.3	0.01	0.01	0.02	0.02	4.3	0.01	0.01	0.01	0.01
Other Homoptera	0	0	0	0	0	8.3	0.14	0.14	0.61	0.61	21.7	0.20	0.13	0.72	0.45
Heteroptera	91.4	10.20	1.62	39.18	5.59	91.7	17.15	3.58	49.67	7.56	95.7	6.73	0.91	28.85	3.87
Total Hymenoptera[d]	*100*	*25.35*	*3.29*	*100*		*100*	*19.46*	*2.84*	*100*		*100*	*22.58*	*2.54*	*100*	
Formicidae	100	25.14	3.30	98.56	0.80	100	18.29	2.90	93.36	4.57	100	21.71	2.44	96.63	0.70
Other Hymenoptera	20	0.22	0.12	1.44	0.80	41.7	1.17	0.71	6.64	4.57	69.6	0.87	0.17	3.37	0.70

[a] Number of broods (n) = 35, Number of roost sites (n) = 95 (Roost sites per brood: Range = 1-12, 2.70 ± 0.49, $\bar{x} \pm$ SE). [b] Number of broods (n) = 12, Number of roost sites (n) = 75 (Roost sites per brood: Range = 1-12, 6.25 ± 1.15, $\bar{x} \pm$ SE). [c] Number of broods (n) = 23, Number of roost sites (n) = 132 (Roost sites per brood: Range = 1-10, 5.70 ± 0.64, $\bar{x} \pm$ SE). [d] Adults unless stated larvae.

Table 5.2. Mean percentage (by numbers) of invertebrate groups in the diet of northern bobwhite chicks on Pebble Hill Plantation in southern Georgia, United States, 2002-2004. Faecal samples were collected from nocturnal roost sites of broods with a radio-collared adult until 14 days old.

Invertebrate Group	Year														
	2002[a]					2003[b]					2004[c]				
	% occurrence in broods	% in samples				% occurence in broods	% in samples				% occurence in broods	% in samples			
		Overall		Within groups			Overall		Within groups			Overall		Within groups	
		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Araneae	86.7	4.13	0.79			100	13.35	2.36			100	7.67	2.62		
Diptera[d]	46.7	0.75	0.22			42.9	0.55	0.37			42.9	1.57	1.00		
Isoptera	0	0	0			28.6	0.06	0.04			28.6	0.29	0.25		
Lepidoptera – larvae	80	1.77	0.50			85.7	1.17	0.46			57.1	1.10	0.51		
Neuroptera – larvae	26.7	0.33	0.19			0	0	0			0	0	0		
Orthoptera	93.3	7.36	1.11			100	3.62	0.59			100	10.75	2.00		
Total Coleoptera[d]	*100*	*43.54*	*4.98*	*100*		*100*	*44.74*	*7.22*	*100*		*100*	*43.50*	*5.65*	*100*	
Cantharidae	0	0	0	0	0	14.3	0.08	0.08	0.24	0.24	0	0	0	0	0
Carabidae – adults	86.7	1.22	0.27	4.36	1.17	71.4	1.26	1.05	3.94	3.22	71.4	1.39	0.65	3.45	1.82
Carabidae – larvae	13.3	0	0	0	0	14.3	0	0	0	0	42.9	0.64	0.36	1.62	1.00
Chrysomelidae – adults	100	7.09	1.75	18.84	3.92	100	13.29	1.49	33.49	4.99	100	18.27	4.01	45.72	9.81
Chrysomelidae – larvae	73.3	0.98	0.33	2.57	0.86	14.3	0.09	0.09	0.36	0.36	0	0	0	0	0
Curculionidae	100	30.35	5.87	62.39	6.55	100	28.40	7.16	57.26	6.69	100	21.33	6.44	44.56	9.68
Elateridae	0	0	0	0	0	14.3	0	0	0	0	0	0	0	0	0
Scarabidae	0	0	0	0	0	42.9	0.12	0.07	0.39	0.21	28.6	0.17	0.11	0.34	0.24
Staphylinidae	13.3	0.07	0.05	0.28	0.25	14.3	0.03	0.03	0.05	0.05	0	0	0	0	0
Other – adults	100	3.45	1.02	9.88	2.77	100	1.38	0.22	4.17	1.17	100	1.60	0.22	4.08	0.74
Others – larvae	20	0.39	0.24	1.68	1.09	14.3	0.08	0.08	0.11	0.11	14.2	0.10	0.10	0.25	0.25
Total Hemiptera	*100*	*21.45*	*3.28*	*100*		*100*	*24.08*	*5.87*	*100*		*100*	*13.18*	*3.07*	*100*	
Homoptera	86.7	8.32	1.84			100	8.83	3.50			100	6.09	1.67		
Aphididae	80	3.87	1.52	17.92	5.82	71.4	1.00	0.41	7.38	3.57	71.4	1.18	0.46	11.14	5.74
Cicadellidae	86.7	3.00	0.56	12.90	2.23	100	3.34	1.49	12.34	3.63	85.7	3.11	1.17	21.88	5.29
Cercopidae	60	1.40	0.67	5.02	1.96	100	4.30	2.04	15.35	4.32	71.4	1.53	0.56	9.09	2.55
Delphacidae	20	0.05	0.03	0.20	0.12	0	0	0	0	0	14.2	0.18	0.18	0.93	0.93
Other Homoptera	0	0	0	0	0	42.9	0.20	0.11	0.81	0.38	14.2	0.08	0.08	1.07	1.07
Heteroptera	100	13.13	2.34	63.95	5.72	100	15.25	4.13	64.12	7.44	100	7.09	1.55	55.88	5.71
Total Hymenoptera[d]	*100*	*20.68*	*2.46*	*100*		*100*	*12.44*	*1.09*	*100*		*100*	*21.94*	*4.28*	*100*	
Formicidae	100	20.64	2.44	99.89	0.11	100	12.08	1.17	96.64	2.04	100	19.97	3.94	92.71	4.41
Other Hymenoptera	6.7	0.04	0.04	0.11	0.11	42.9	0.36	0.19	3.36	2.04	57.1	1.97	1.40	7.29	4.41

[a] Number of broods (n) = 15, Number of roost sites (n) = 88 (Roost sites per brood: Range = 1-11, 5.87 ± 1.10, $\bar{x}$ ± SE). [b] Number of broods (n) = 7, Number of roost sites (n) = 49 (Roost sites per brood: Range = 2-9, 7.00 ± 0.93, $\bar{x}$ ± SE). [c] Number of broods (n) = 7, Number of roost sites (n) = 40 (Roost sites per brood: Range = 3-10, 5.70 ± 0.81, $\bar{x}$ ± SE). [d] Adults unless stated larvae.

Table 5.3. Mean percentage (by numbers) of invertebrate groups in the diet of northern bobwhite chicks on farmland in central Georgia, United States, 2002 and 2003. Faecal samples were collected from nocturnal roost sites of broods with a radio-collared adult until 14 days old.

Invertebrate Group	Year									
	2002[a]					2003[b]				
	% occurrence in broods	% in samples				% occurrence in broods	% in samples			
		Overall		Within groups			Overall		Within groups	
		$\bar{x}$	SE	$\bar{x}$	SE		$\bar{x}$	SE	$\bar{x}$	SE
Araneae	93.3	2.11	0.35			100	5.60	1.63		
Diptera[c]	86.7	2.16	0.65			50	0.70	0.54		
Isoptera	0	0	0			0	0	0		
Lepidoptera – larvae	100	12.58	2.75			100	7.36	1.82		
Neuroptera – larvae	13.3	0.04	0.03			0	0	0		
Orthoptera	100	5.99	1.44			100	10.26	3.49		
Total Coleoptera[c]	*100*	*27.55*	*2.55*	*100*		*100*	*21.03*	*4.36*	*100*	
Cantharidae	0	0	0	0	0	50	0.20	0.20	0.84	0.5
Carabidae – adults	93.3	2.21	0.67	7.57	2.22	100	4.62	2.11	21.80	7.87
Carabidae – larvae	6.7	0.09	0.09	0.27	0.27	0	0	0	0	0
Chrysomelidae - adults	100	7.83	1.44	27.96	3.63	100	6.85	2.94	30.39	8.28
Chrysomelidae - larvae	86.7	2.66	0.96	8.20	2.52	50	0.78	0.57	3.26	2.42
Curculionidae	100	11.30	1.52	42.91	4.21	100	7.11	1.66	33.87	2.26
Elateridae	6.7	0.01	0.01	0.02	0.02	0	0	0	0	0
Scarabidae	0	0	0	0	0	25	0.11	0.11	0.47	0.47
Staphylinidae	40	0.30	0.14	1.03	0.48	25	0.04	0.04	0.18	0.18
Other – adults	100	3.15	0.56	12.00	2.12	100	1.31	0.33	9.18	4.93
Other – larvae	6.7	0.02	0.02	0.05	0.05	0	0	0	0	0
Total Hemiptera	*100*	*30.39*	*3.90*	*100*		*100*	*45.32*	*10.17*	*100*	
Homoptera	100	7.15	2.25			100	6.20	1.09		
Aphididae	40	0.27	0.11	1.68	0.75	75	0.32	0.15	0.84	0.33
Cicadellidae	93.3	4.15	1.92	13.93	3.93	100	4.84	1.21	10.90	1.89
Cercopidae	60	2.72	1.69	6.55	3.45	100	1.04	0.24	2.51	0.77
Delphacidae	0	0	0	0	0	0	0	0	0	0
Other Homoptera	0	0	0	0	0	0	0	0	0	0
Heteroptera	100	23.24	3.07	77.84	4.27	100	39.12	9.12	85.74	1.33
Total Hymenoptera[c]	*100*	*19.17*	*2.71*	*100*		*100*	*9.74*	*3.75*	*100*	
Formicidae	100	19.06	2.71	99.45	0.47	100	9.38	3.42	98.20	1.80
Other Hymenoptera	13.3	0.11	0.09	0.55	0.47	25	0.36	0.36	1.80	1.80

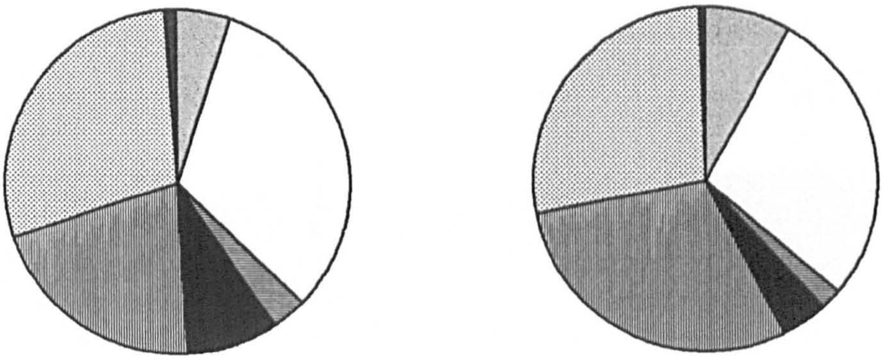
[a] Number of broods (*n*) = 15, Number of roost sites (*n*) = 70 (Roost sites per brood: Range = 1-7, 4.67 ± 0.45, $\bar{x}$ ± SE). [b] Number of broods (*n*) = 4, Number of roost sites (*n*) = 19 (Roost sites per brood: Range = 2-7, 4.75 ± 1.03, $\bar{x}$ ± SE). [c] Adults unless stated larvae.

0.398, $P = 0.691$) or Hemiptera (TTRS: $\Lambda = 0.813$, $F_{2,21} = 2.412$, $P = 0.114$, PH: $\Lambda = 0.730$, $F_{2,9} = 1.667$, $P = 0.242$) (Figures 5.2 and 5.3). The Farmland data were too sparse to examine for differences within Hemiptera.

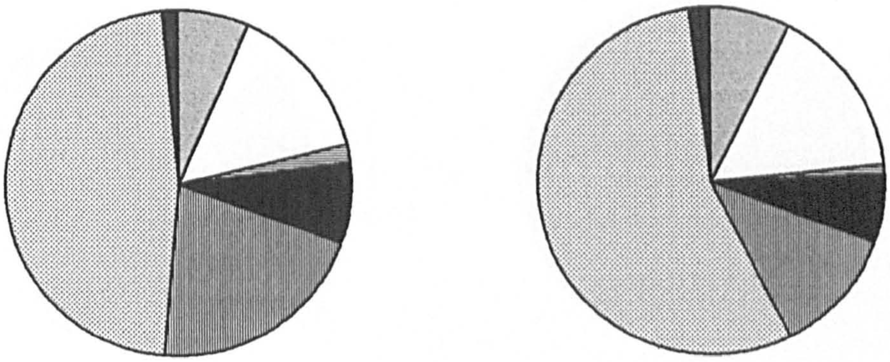
3.3 Annual differences on TT and PH

As age did not influence invertebrate composition in the diet of chicks, all faecal samples for each brood were pooled. Log-ratios were then calculated for each brood in all years. Including year as a factor, differences in diet composition of broods between years on TTRS (2002: $n = 35$, 2003: $n = 12$, 2004: $n = 23$) and PH (2002: $n = 15$, 2003: $n = 7$, 2004: $n = 7$) were examined separately using MANOVA. On the farmland, data were collected from an insufficient number of broods in 2003 to allow between year differences to be examined. If a significant difference was found, a ranking matrix was produced to determine where the differences lay (Aebischer *et al.* 1999). The differences between samples for all possible pairs of log-ratios were examined using *t* tests. The relative abundance of the six invertebrate orders in the diet of chicks did not vary between years on TT ($\Lambda = 0.823$, $F_{10,126} = 1.291$, $P = 0.242$) (Table 5.1) or PH ($\Lambda = 0.535$, $F_{10,44} = 1.613$, $P = 0.134$) (Table 5.2). No yearly variations in the relative abundance of the different prey items within the order Hemiptera were also found on either TTRS ($\Lambda = 0.917$, $F_{4,128} = 1.414$, $P = 0.233$) or PH ($\Lambda = 0.810$, $F_{4,50} = 1.386$, $P = 0.252$). However, the composition of prey items within the Order Coleoptera varied significantly between years on both TTRS ($\Lambda = 0.820$, $F_{4,132} = 3.440$, $P = 0.010$) and PH ($\Lambda = 0.640$, $F_{4,50} = 3.124$, $P = 0.023$). On TTRS there was a difference in diet composition between 2002 and 2004 ($\Lambda = 0.831$, $F_{2,55} = 5.578$, $P = 0.006$) with, relative

1). Tall Timbers Research Station



2). Pebble Hill Plantation



3). Farmland

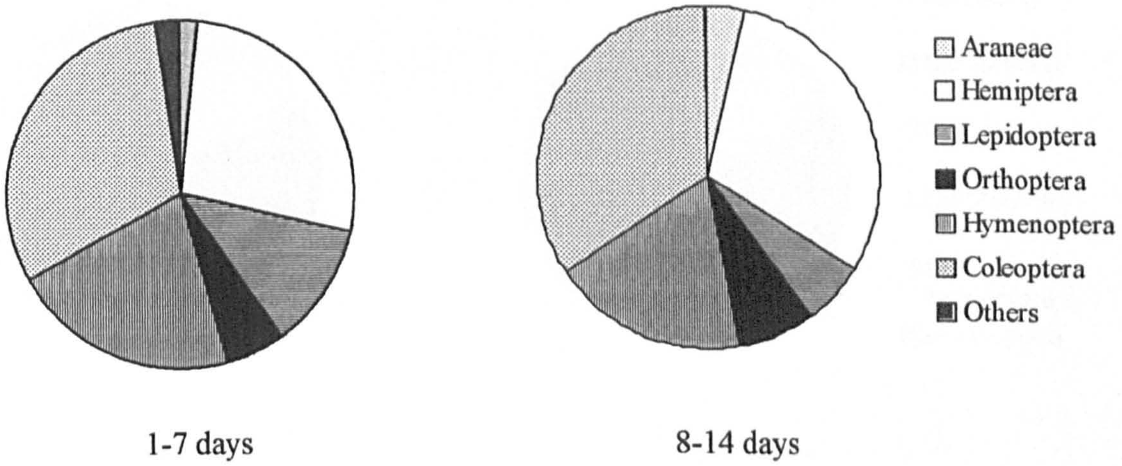


Figure 5.1. The composition (by numbers) of invertebrate orders in the diet of northern bobwhite chicks aged 1-7 days and 8-14 days on 1). Tall Timbers Research Station, Florida, 2002-2004, (*n* = 23 broods). 2). Pebble Hill Plantation, Georgia, 2002-2004, (*n* = 11 broods). 3). Farmland in central Georgia, 2002-2003, (*n* = 7 broods). Only broods where faecal matter was collected in both age categories were included. The Coleoptera group contained both adults and larvae. The Lepidoptera group contained only larvae.

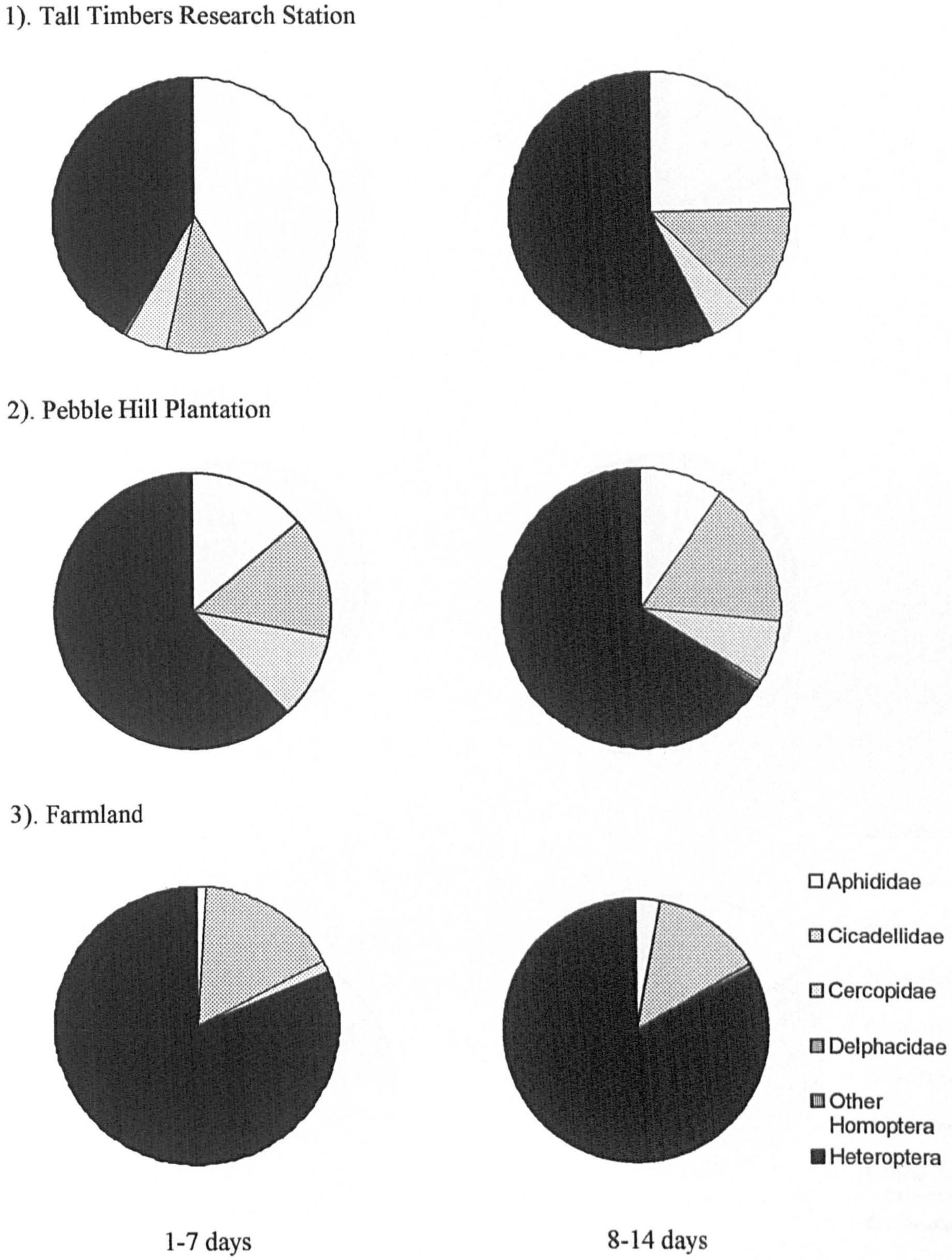
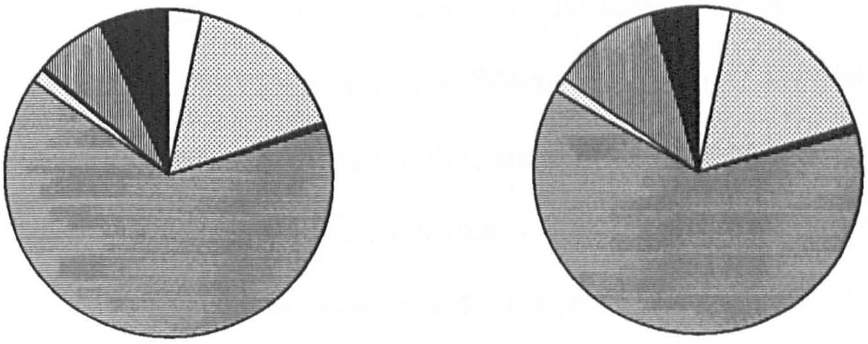
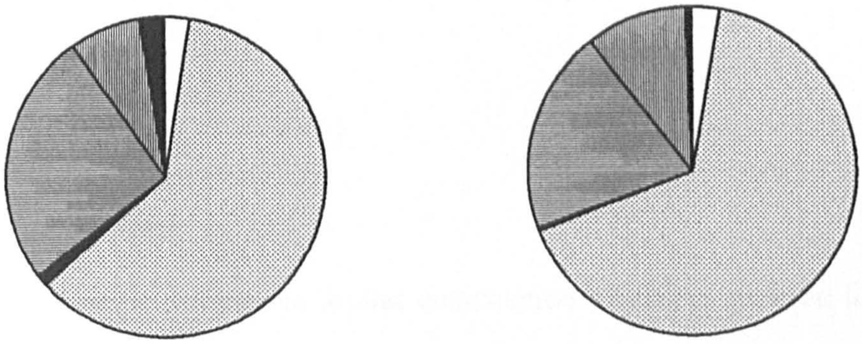


Figure 5.2. The composition (by numbers) of invertebrate groups within the order Hemiptera in the diet of northern bobwhite chicks aged 1-7 days and 8-14 days on 1). Tall Timbers Research Station, Florida, 2002-2004, (*n* = 23 broods). 2). Pebble Hill Plantation, Georgia, 2002-2004. (*n* = 11 broods). 3). Farmland in central Georgia, 2002-2003. (*n* = 7 broods). Only broods where faecal matter was collected in both age categories were included.

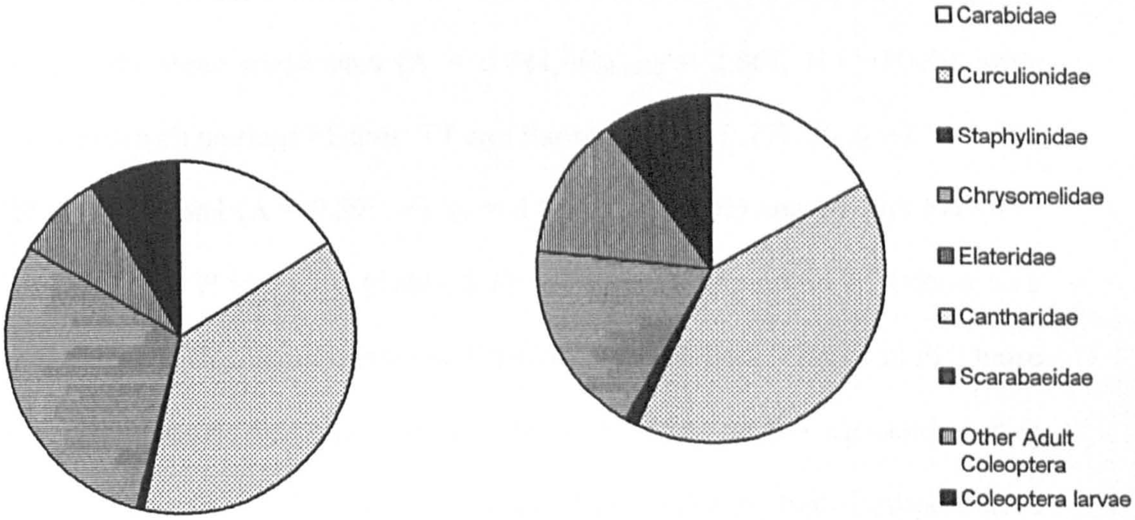
1). Tall Timbers Research Station



2). Pebble Hill Plantation



3). Farmland



1-7 days 8-14 days

Figure 5.3. The composition (by numbers) of invertebrate groups within the order Coleoptera in the diet of northern bobwhite chicks aged 1-7 days and 8-14 days on 1). Tall Timbers Research Station, Florida, 2002-2004, (n = 23 broods). 2). Pebble Hill Plantation, Georgia, 2002-2004. (n = 11 broods). 3). Farmland in central Georgia, 2002-2003. (n = 7 broods). Only broods where faecal matter was collected in both age categories were included.

to Curculionidae, greater numbers of Chrysomelidae eaten in 2004 than 2002 (t_{56} = -3.233, $P = 0.002$). On PH diet composition differed between 2002 and 2003 ($\Lambda = 0.671$, $F_{2,19} = 4.666$, $P = 0.022$) and between 2002 and 2004 ($\Lambda = 0.710$, $F_{2,19} = 3.874$, $P = 0.039$). Relative to Chrysomelidae, more Others were eaten in 2002 than in 2003 ($t_{20} = 2.954$, $P = 0.008$). A greater number of Curculionidae ($t_{20} = 2.137$, $P = 0.045$) and Others ($t_{20} = 2.529$, $P = 0.020$) were also eaten in 2002 than in 2004 relative to Chrysomelidae.

3.4 Site differences

3.4.1 Between orders

To examine differences in diet composition of chicks between the three study sites, data from 2002 and 2003 were pooled on each site (TTRS: $n = 47$, PH: $n = 22$, Farmland: $n = 19$). At the order level, invertebrate composition of the diet of chicks varied between the three study sites ($\Lambda = 0.784$, $F_{10,222} = 2.867$, $P = 0.002$), with differences between all pairings of sites; TT and Farmland ($\Lambda = 0.753$, $F_{5,60} = 3.944$, $P = 0.004$), PH and Farmland ($\Lambda = 0.590$, $F_{5,35} = 4.858$, $P = 0.002$) and TT and PH ($\Lambda = 0.826$, $F_{5,63} = 2.658$, $P = 0.030$) (Table 5.4). While the proportion of Others was significantly higher in the diet of chicks on Farmland than on both TTRS and PH, more Hymenoptera were eaten by chicks on the plantations than on the agricultural area (Tables 5.1-5.3). The diet of chicks on PH contained a significantly higher proportion of Coleoptera but significantly less Hemiptera than chicks on both TTRS and Farmland (Tables 5.1-5.3).

Table 5.4. Relative differences in the abundance of invertebrate orders in the diet of northern bobwhite chicks on Tall Timbers Research Station, Florida, Pebble Hill Plantation, Georgia, and on Farmland, Georgia, United States, 2002-2003. Groups are ranked in order of their relative abundance in the diet of chicks from the first site in each pair.

Ranking	Tall Timbers: Farmland	Pebble Hill: Farmland	Tall Timbers: Pebble Hill
1	Hymenoptera^{a}	Coleoptera^{a}	Hemiptera^{a}
2	Hemiptera^{a}	Hymenoptera^{a}	Hymenoptera^{ac}
3	Coleoptera^{a}	Araneae^{ac}	Orthoptera^{ad}
4	Orthoptera^{a}	Orthoptera^{ac}	Coleoptera^{bcd}
5	Araneae^{a}	Hemiptera^{bc}	Araneae^{bcd}
6	Others^{b}	Others^{b}	Others^{bd}

Within pairs, different letters between orders indicate significant differences at the 5% level.

3.4.2 Within orders

Hemiptera

The invertebrate composition within the Order Hemiptera varied significantly between the three sites ($\Lambda = 0.765$, $F_{4, 166} = 5.959$, $P = 0.000$). Differences were found between TTRS and Farmland ($\Lambda = 0.734$, $F_{2, 62} = 11.249$, $P = 0.000$) and PH and Farmland ($\Lambda = 0.852$, $F_{2, 37} = 3.225$, $P = 0.050$) but not between TTRS and PH ($\Lambda = 0.918$, $F_{2, 66} = 2.935$, $P = 0.060$) (Table 5.5). Compared with chicks on TTRS and PH, chicks on Farmland ate significantly more Heteroptera relative to both Aphididae and Other Homoptera.

Table 5.5. Relative differences in the abundance of Hemipteran groups in the diet of northern bobwhite broods on Tall Timbers Research Station, Florida, (*n* = 46) Pebble Hill Plantation, Georgia, (*n* = 22) and on Farmland, Georgia (*n* = 19), United States, 2002-2003. Groups are ranked in order of their relative abundance in the diet of chicks from the first site in each pair.[a]

Ranking	Tall Timbers: Farmland	Pebble Hill: Farmland	Tall Timbers: Pebble Hill
1	Aphididae[a]	Aphididae[a]	NS
2	Other Homoptera[b]	Other Homoptera[b]	
3	Heteroptera[c]	Heteroptera[c]	

[a] Within pairs, different letters between orders indicate significant differences at the 5% level.

Coleoptera

The composition of the prey items within the Coleoptera Order differed significantly between sites (Λ = 0.748, $F_{4,\ 168}$ = 6.550, P = <0.001). Composition differences were found between all pairings of sites; TT and Farmland (Λ = 0.759, $F_{2,\ 66}$ = 10.475, P = 0.000), PH and Farmland (Λ = 0.774, $F_{2,\ 38}$ = 5.540, P = 0.008) and TT and PH (Λ = 0.885, $F_{2,\ 63}$ = 4.075, P = 0.022) (Table 5.6). The diet of chicks on PH contained significantly more Curculionidae relative to Chyrsomelidae than that of chicks on both TTRS and Farmland. Relative to Curculionidae, more Others were eaten on Farmland than on PH.

Table 5.6. Relative differences in the abundance of Coleopteran groups in the diet of northern bobwhite broods on Tall Timbers Research Station, Florida, (*n* = 47), Pebble Hill Plantation, Georgia, (*n* = 22) and on Farmland, Georgia (*n* = 19), United States, 2002-2003. Groups are ranked in order of their relative abundance in the diet of chicks from the first site in each pair.[a]

Ranking	Tall Timbers: Farmland	Pebble Hill: Farmland	Tall Timbers: Pebble Hill
1	Chrysomelidae[a]	Curculionidae[a]	Chrysomelidae[a]
2	Curculionidae[b]	Chrysomelidae[b]	Other[ab]
3	Other[ab]	Other[b]	Curculionidae[b]

[a] Within pairs, different letters between orders indicate significant differences at the 5% level.

3.5 Between site differences in chick-growth rates and survival

After removing broods due to mixing and/ or missed or failed brood captures, data were sparse on some sites in some years. Therefore, between site differences in chick growth rates and survival were examined by pooling data collected between 2002-2003 on each site.

3.5.1 Growth rates

Between 2002-2003, chick growth rate data were collected from 14 broods on TTRS (2002: n = 10, 2003: n = 4), 14 broods on PH (2002: n = 11, 2003: n = 3) and seven broods on Farmland (2002: n = 6, 2003: n = 1). After accounting for the effect of year, the daily growth rates of chicks did not differ between sites ($F_{2,31} = 1.926$, $P = 0.163$) (Figure 5.4).

3.5.2 Variation in growth rates within broods

To investigate whether the variance in chick growth rates within broods differed between sites, the within-brood coefficient of variation (CV; standard deviation divided by the mean) of chick-growth rates was calculated for broods captured between 2002-2003 with ≥2 chicks. Although the mean within-brood CV of growth rates was greatest on Farmland (0.274 ± 0.05; n = 7), it did not differ significantly from that found on PH (0.175 ± 0.04; n = 13) or TTRS (0.201 ± 0.04; n = 12) after controlling for year ($F_{2,28} = 1.384$, $P = 0.267$).

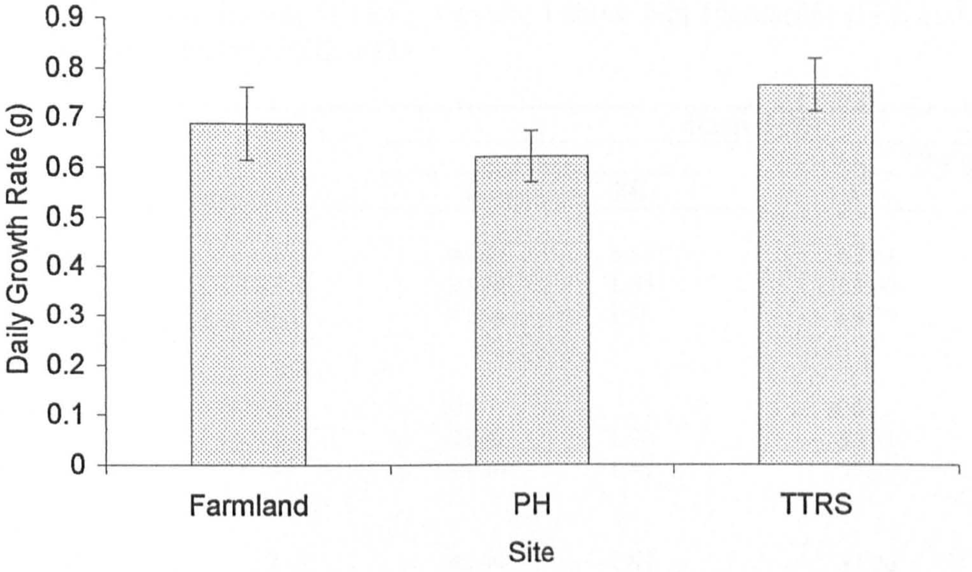


Figure 5.4. Mean (±1 SE) daily growth rates of northern bobwhite chicks from hatching to 10 days in broods (*n*) on Tall Timbers Research Station (TTRS) (n = 14), Florida, Pebble Hill Plantation (PH) (n = 14) and Farmland (n = 7), Georgia, United States, 2002-2003. Values presented are corrected for the effect of year.

3.5.3 Survival

Between 2002-2003, chick survival data were collected from 24 broods on TTRS (2002: n = 19, 2003: n = 5), 15 broods on PH (2002: n = 12, 2003: n = 3) and seven broods on Farmland (2002: n = 6, 2003: n = 1). Although percentage chick survival from hatching to 10 days was 18 % higher on Farmland than on PH (Table 5.7), daily chick survival did not differ significantly between the three study sites after the effect of year was accounted for ($F_{2,42}$ = 1.322, P = 0.277).

Table 5.7. Daily and 10-day percentage survival of northern bobwhite chicks on Tall Timbers Research Station (TTRS), Florida, Pebble Hill Plantation (PH) and Farmland, Georgia, United States, 2002-2003.

		Survival (%)			
Year	*n*	Daily		10-day[a]	
Site		$\bar{x}$	SE	$\bar{x}$	SE
2002					
Farmland	6	94.63	1.67	61.81	11.05
PH	12	92.72	1.55	53.06	7.56
TTRS	19	93.64	1.42	59.77	6.07
2003					
Farmland	1	100		100	
PH	3	89.42	2.90	35.81	11.11
TTRS	5	93.40	1.57	53.09	8.49
Pooled					
Farmland	7	95.40	1.61	67.26	10.81
PH	15	92.06	1.37	49.61	6.55
TTRS	24	93.59	1.16	58.37	5.08

[a] % survival = $[(\mathrm{DSR})^{10} \times 100]$

3.6 Effect of invertebrates on chick-growth rates and survival

3.6.1 Growth rates

A total of 47 broods (TTRS: $n = 24$, PH: $n = 16$, Farmland: $n = 7$) that hatched between 2002 and 2004 provided data that were used to investigate relationships between the growth rates of chicks and the composition of invertebrates in the diet.

In a stepwise multiple regression analysis, Others was the only invertebrate group to have a significant effect on chick growth rates ($F_{1,45} = 5.074$, $P = 0.029$). Because site-year was non-significant and was therefore removed from the model, a multiple regression analysis was then performed where only Others and site-year were included in the model. In this analysis, the significant negative relationship between the proportion of Others in the diet and daily chick growth rates remained ($t_{44} = -2.074$, $P = 0.044$). Again, site-year was non-significant. Chick growth rates were not related to the collective proportion of important invertebrate groups in the diet after adjusting for site-year in a multiple regression (t_{44} = -0.168, P = 0.868).

3.6.2 Variation in chick growth rates within broods

Others and Homoptera were both found to have a significant positive effect on the variance of chick growth rates within broods (P = <0.02), following a forward stepwise multiple regression analysis. Because site-year was again non-significant, a separate analysis was performed where only Others, Homoptera and site-year were included in the model. This multiple regression again showed that variation in the growth rates of chicks within broods was positively related to the proportion of Others and Homoptera in the diet of broods ($F_{2,38}$ = 3.997, P = 0.015, r^2 = 0.245). Site-year was non-significant. Conversely, when the relationship between the collective proportion of important invertebrate items in the diet and the variation in growth rates of chicks within broods was investigated, a significant negative correlation was found after the effect of site-year was accounted for (t_{38} = -2.601, P = 0.013) (Figure 5.5).

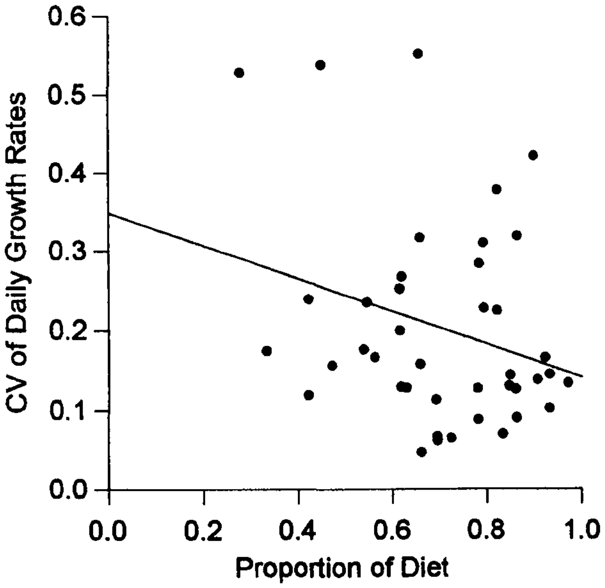


Figure 5.5. Relationship between the within-brood coefficient of variation (CV; standard deviation divided by the mean) of mean daily growth rates of northern bobwhite chicks from hatching to 10 days (range 8-12 days) in relation to the collective proportion of Coleoptera and Heteroptera in their diet. Broods were captured between 2002-2004 on Farmland ($n = 7$) and on Pebble Hill Plantation ($n = 14$) in Georgia and on Tall Timbers Research Station ($n = 20$) in Florida, United States.

3.6.3 Survival

Between 2002 and 2004, a total of 58 broods (TTRS: $n = 34$, PH: $n = 17$, Farmland: $n = 7$) provided data on diet together with an estimate of daily survival.

The stepwise regression revealed that none of the invertebrate groups entered into the model had a significant effect on the survival of chicks. There was also no relationship between chick survival and the collective proportion of important invertebrate groups in the diet when the effect of site-year was accounted for ($t_{55} = -0.851, P = 0.398$).

4.0 DISCUSSION

This study represents one of the largest dietary studies ever conducted on a gamebird species in the United States. Unlike previous studies that only examined diet composition of bobwhite chicks in one small area, this study also compared the diet of chicks within stable and declining bobwhite populations in different landscapes. As Gullion (1966) commented '.....to be of significance in developing long-range management policy, studies of food habits must deal with the critical period of each year and they must compare the foods and feeding habits of birds living in populations showing increasing densities as well as stable and declining numbers (Gullion 1966).'

4.1 Diet composition

Three of the most selected prey items of bobwhite chicks, Coleoptera, Hemiptera and Hymenoptera, (Table 4.4), formed over 70% of the invertebrate diet of chicks on all sites and in all years. The most selected prey item, Coleoptera, has often been reported as one of the most numerically important prey groups in the invertebrate-diet of both wild and captive-reared bobwhite chicks, irrespective of the habitat type in which they were foraging (Stoddard 1931, Hurst 1972, Jackson *et al.* 1987, Palmer 1995). Although Coleoptera were abundant in the diet on all sites, fewer were eaten by chicks on TTRS and Farmland than on PH, where this prey group accounted for over 40% of the invertebrate-diet in all years. The high proportion of Curculionidae found in the diet of chicks on PH is consistent with bobwhite and other gamebird chicks that have been foraging in grass dominated habitats (Ford *et al.* 1938, Hurst 1972). Therefore, the large areas of wiregrass, *Aristida stricta*, that were only present on PH may harbour high densities of Curculionidae species. In a study where the stomachs of captive-reared bobwhite chicks were examined after foraging in non-cropped weedy fields, Chrysomelidae and Caribidae were the predominant Coleoptera families eaten (Jackson *et al.* 1987). Between the plantations, non-cropped weedy fields were most abundant on TTRS where chicks also ate a significantly higher proportion of Chrysomelidae relative to Curculionidae than on PH.

Consistent with previous dietary studies of wild bobwhite chicks, high numbers of Hemiptera were found in the diet on all sites (Stoddard 1931, Hurst 1972). In a study by Hurst (1972), Hemiptera were found to be the second most abundant prey group in the invertebrate-diet of wild chicks foraging in forested landscapes. Captive-reared bobwhite chicks have also been found to eat high numbers of Hemiptera when foraging in both forested and agricultural landscapes (Hurst 1972, Palmer 1995). In this study, a significantly greater proportion of Hemiptera were found in the diet of chicks on TTRS and Farmland than on PH. This difference between the plantations may be due to a higher prevalence of disked, non-cropped weedy fields and burned old-field habitat on TTRS than on PH. These habitats are known to harbour some of the highest densities of Hemiptera found on plantations in this region (DeVos and Mueller 1993, Manley *et al.* 1994, Hammond 2001). Broods on the farmland site often use non-cropped, fallow fields, weedy marginal habitats and the 6m non-sprayed headlands surrounding cropped fields (Cook 2004). Again, these types of habitat can harbour high densities of Hemiptera, particularly the sub-order Heteroptera (Rands 1985, Chiverton and Sotherton 1991, Palmer 1995).

Due to the lack of detail in which the diets of bobwhite chicks have been previously described, the value of Aphididae as a dietary item has never been recognised

(Stoddard 1931, Hurst 1972, Jackson *et al.* 1987). In dietary studies of grey partridge chicks on farmland in Great Britain, Aphididae have been found to contribute a high proportion to the invertebrate component of the diet (Ford *et al.* 1938, Vickerman and O'Bryan 1979, Green 1984). However, in this study bobwhite chicks on farmland ate significantly less Aphididae relative to all other groups within Hemiptera than chicks on the plantations. The high use of pesticides on agricultural landscapes in the southeastern United States over the last 50 years may have had a more detrimental effect on Aphididae populations than other Hemipteran species in farmland habitats (Aebischer and Potts 1990). An examination of historical pest monitoring data may indicate such a trend.

During the early 1930's, very few ants (recorded as trace) were found in the crops and gizzards of 20 wild bobwhite chicks captured on plantations in northern Florida and southern Georgia (Stoddard 1931). In most years of this study, Hymenoptera, of which over 90% were Formicidae, accounted for approximately 20% of the invertebrates in the diet of chicks on both TTRS and PH. The abundance of Formicidae in chick foraging habitats in this region may have increased over the last 70 years due to changes in habitat management techniques (Brennan 1993) or because of the colonisation of the area by fire ants, *Solenopsis spp.*, (Porter and Savignano 1990). Although in this study Formicidae were not identified to species, Hurst (1972) reported that the Formicidae found in the stomachs of captive-reared chicks after foraging were mostly fire ants. Because it has been shown that the colonization of an area by fire ants negatively impacts on invertebrate diversity and abundance (Porter and Savignano 1990), it has been hypothesized that fire ants may reduce the abundance of bobwhite chick prey items in foraging habitats (Allen *et al.* 1993). Consequently, the invertebrate composition in the diet of bobwhite chicks in the southeastern United States could have altered since being colonized by fire ants. The effect this has had on chick survival and subsequent bobwhite populations should be investigated and, if found to be adverse, effective fire ant control strategies should be developed.

4.2 Chick age

While it has been reported that the proportion of invertebrate matter in the diet of bobwhite chicks decreases over the first two weeks of age (Stoddard 1931), this study found no evidence that the composition within this component of the diet also changes during this period. Although the effect of chick age on the composition of invertebrates in the diet of wild bobwhite chicks has never previously been examined, a field study using captive reared bobwhite chicks suggests that invertebrate selection may only change after two weeks of age (Jackson *et al.* 1987). In particular, Jackson *et al.* (1987) reported that captive reared chicks foraging in various brood-rearing habitats had a greater preference for Hymenoptera after 14 days old. In agreement with this finding, the proportion of Formicidae in the diet of grey partridge chicks has also been found to increase rapidly after two weeks of age (Ford *et al.* 1938, Vickerman and O'Bryan 1979). To determine if the composition of invertebrates in the diet of wild bobwhite chicks changes after two weeks of age, future dietary studies should continue collecting faecal samples from broods until they are 3-4 weeks of age.

4.3 Chick growth

While both laboratory and field dietary studies of gamebird chicks have demonstrated that chick-growth is related to the proportion of invertebrates in the diet (Dahlgren 1990, Palmer 1995, Park *et al.* 2001, Liukkonen-Anttila *et al.* 2002, Southwood and Cross 2002), few have examined the effect of invertebrate composition on chick-condition (Borg and Toft 2000). In this study, the mean chick-growth rate within broods was negatively related to the proportion of the group Others, consisting mainly of Lepidoptera larvae, in the diet. This is surprising given that Lepidoptera larvae have been previously described as an important prey item of chicks of bobwhite (Stoddard 1931, Jackson *et al.* 1987) and other gamebirds (Green 1984, Hill 1985, Picozzi *et al.* 1999). Similarly, the value of Aphididae in the diet of grey partridge is also unclear. In field studies, some researchers have found it to be an important prey item (Green 1984, Itamies *et al.* 1996) while others did not (Potts 1986, Panek 1992). To help explain these contradictory results, Borg and Toft (2000) conducted a feeding trial where grey partridge chicks were given one of three diets containing Aphididae, Orthoptera or a mixture of both. They found that the chicks fed only Aphididae had significantly lower growth rates than chicks fed Orthoptera. However, when Orthoptera were supplemented with Aphididae, chick growth rates were significantly higher than those fed only Orthoptera. From these results, Borg and Toft (2000) concluded that while Aphididae are a poor dietary item in isolation, a small proportion within the diet of chicks might provide some nutritional benefit. A similar phenomenon may also occur with Lepidoptera larvae in the diet of bobwhite chicks. Furthermore, the results of this study also suggest that, in certain conditions, competition between chicks may further exacerbate this problem. The relationships found in this study between chick growth-variance within broods and diet (Figure 5.5) suggest that when chicks are foraging in habitat patches where there is an insufficient availability of preferred prey items, the weaker chicks in a brood may eat a higher proportion of non-preferred items relative to their stronger siblings. These differences in diet would then result in differential growth rates between chicks within the same brood. Although not significantly different, the greater variation in growth rates of chicks within broods found on the Farmland site could indicate that broods on this landscape use more habitat patches with low availabilities of important items than on plantations. This is consistent with previous radio-tracking studies on plantations that have suggested that bobwhite broods on these landscapes select for habitat patches with high numbers of Coleoptera and Hemiptera, and do not use areas with high numbers of Lepidoptera larvae (Hammond 2001, DeVos and Mueller 1993).

4.4 Chick survival

Although bobwhite biologists have suggested that the decline in bobwhite populations on agricultural landscapes has been partly caused by a reduction in chick survival (Brennan 1991), this study found no difference in chick survival to 10 days between broods on farmland and those on plantations. The survival rates found on all sites in this study are comparable to those previously reported on plantations in southern Georgia and northern Florida (DeVos and Mueller 1993, Hammond 2001). In an extensive study of chick survival on eight plantations in this region, Hammond (2001) reported 10-day chick survival rates of 29.8 and 52.2 % in 1998 and 1999 respectively.

In another study conducted on TTRS between 1984 and 1986, 38% of chicks survived until two weeks old (DeVos and Mueller 1993). On other landscapes, Cantu and Everett (1982) reported 51% of chicks surviving from hatching until two weeks old on pastureland in south Texas, while DeMaso *et al.* (1997) found that 37.9% of chicks reached 20 days of age on a wildlife management area in Oklahoma. Although bobwhite chick survival on arable farmland has not been previously reported, a study on the survival of pheasant chicks on agricultural landscapes in Illinois found that 54% of chicks in broods survived until 5-6 weeks old (Warner *et al.* 1984). In addition, Warner *et al.* (1984) also reported that chick survival in the same region had declined from an estimated rate of 71% during the early 1950's.

The survival of both grey partridge and pheasant chicks to 21 days has been positively related to the proportion of some invertebrates in their diet (Sotherton *et al.* 1993). In grey partridge, the percentage of chicks surviving in a brood was positively related to the collective proportion of Tenthredinidae larvae and Chrysomelidae in the diet. In this study, although chick growth rates were affected by the composition of invertebrates in the diet, survival to 10 days old was not. These results mirror those reported in feeding trails, where the composition and/ or quantity of invertebrates fed to gamebird chicks ≤10 days old affected growth and feather development but not survival (Dahlgren 1990, Liukkonen-Anttila *et al.* 2002, Southwood and Cross 2002). Because of their inability to fly and thermoregulate until approximately 14 days old, gamebird chicks are considered to be most at risk from predation or hypothermia during the first two weeks of life (Potts 1986). While a high proportion of chicks do die during this period, as this, and other studies have shown, it does not appear that these losses are related to the composition of invertebrates in the diet during this time. However, this may change over the following weeks as indicated by grey partridge and pheasant chick survival studies (Green 1984, Hill 1985). In these studies, the period over which survival was estimated included the period when chicks begin to fly and thermoregulate (Potts 1986). Because a poor invertebrate diet delays the age at which chicks are able to fly and resist chilling, those chicks that have eaten an invertebrate-poor diet during the first few weeks will be more vulnerable to predation and bad weather in the third week than those that have been able to consume a high proportion of preferred invertebrates (Southwood and Cross 2002). Consequently, the invertebrate composition in the diet of bobwhite chicks during the first two weeks of age may affect survival after this period. Due to eating a higher proportion of non-preferred items, chicks on farmland may be more susceptible to predation and bad weather after two weeks than those on plantations. Future research should examine chick survival to at least 21 days.

The consequences of a poor diet during the first few weeks of life may also have long-lasting sub-clinical effects on birds. In recent years, studies into the long-term consequences of a nutritionally poor diet during early development have caused negative immunological, reproductive and morphological effects in adulthood (Dahlgren 1990, Lindström 1999, Ohlsson and Smith 2001, Searcy *et al.* 2004). Dahlgren (1990) reported that grey partridge chicks fed an invertebrate-poor diet as a chick, would have a significantly lower body weight at adulthood than those that were fed an invertebrate-rich diet. In a feeding study conducted by Ohlsson and Smith (2001), adult pheasants that received a low protein diet during the first few weeks of life had smaller tarsus lengths than those birds that received a protein-rich diet as chicks.

Although during this study adult bobwhite were captured over a large area of farmland, most birds that subsequently produced broods were on two farms enrolled in the BQI agri-environmental scheme (Chapter II). As a consequence, much of the data for this study were collected from broods that were using farmland enhanced by conservation field borders and other habitat prescriptions. Therefore, because only 292 cropped fields in Georgia are currently managed under the BQI scheme (www.georgiawildlife.dnr.state.ga.us), it is possible that the diet and fitness of chicks on these farms were not typical for farmland across this state. A comparative study of the diets of chicks on BQI and non-BQI farms would be useful, although, as found in this study it may be difficult due to low numbers of bobwhite on land that is not managed for game and other wildlife.

Irrespective of any positive effects the BQI prescriptions are having on the food supply of bobwhite chicks, low participation by landowners in this scheme means that unmanaged marginal habitats and cropped fields remain the most important brood-rearing habitats on most farms in Georgia. However, with the introduction of genetically modified crops, including maize, *Zea mays*, cotton, *Gossypium hirsutum,* and soya beans, *Glycine max*, that are commonly grown in the southeastern United States, biologists have expressed concern that the management of these crops will further reduce the foraging value of cropped fields to farmland birds (Sutherland and Watkinson 2001, Krapu *et al.* 2004). This was investigated and is the subject of the next chapter.

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CHAPTER VI

NORTHERN BOBWHITE CHICK-PREY INVERTEBRATE ABUNDANCE IN GENETICALLY MODIFIED COTTON

SUMMARY

A reduction in the abundance of chick-invertebrate prey in cropped fields, through the use of pesticides, has been cited as a contributory factor in the decline of bobwhite populations on agricultural landscapes.

Here, a field-scale study was conducted on a farm in Georgia, United States, to examine the abundance of northern bobwhite chick-food invertebrates in two Genetically Modified (GM) varieties of cotton in July, August and September, 2002 - 2003. Half-fields were planted to either herbicide tolerant (HTGM) cotton or 'Staked' cotton that was both insect resistant and herbicide tolerant (SGM).

Overall insecticide use was lower in the SGM cotton. While few differences in whole-season counts were found during 2002, counts of Hemiptera, Total Chick Foods and Total Invertebrates were greater in the SGM cotton during 2003. Although no differences in monthly counts were found in 2002, greater numbers of Hemiptera, Total Chick Foods and Total Invertebrates were found in the SGM cotton in August 2003. Total Chick Foods remained greater in the SGM cotton in September.

This study demonstrates that the management of SGM cotton in comparison to HTGM cotton can result in a greater abundance of invertebrates important in the diet of northern bobwhite chicks and other farmland birds.

1.0 INTRODUCTION

Agricultural intensification has been cited as a major contributory factor in the decline of many farmland bird species in North America (Vance 1976, Church *et al.* 1993, Blackwell and Dolbeer 2001, Murphy 2003), and some European countries (Donald *et al.* 2001), particularly Great Britain (Chamberlain *et al.* 2000, Benton *et al.* 2002, Robinson and Sutherland 2002, Newton 2004). The population declines of gallinaceous birds, most notably grey partridge, *Perdix perdix*, in Great Britain (Potts 1986) and northern bobwhite (henceforth, bobwhite) in the United States (Church *et al.* 1993, Burger 2001), have been dramatic. Although various aspects of modern agriculture have contributed to the decline of bobwhite, those thought to have had most impact are a loss of marginal habitats, changes in crop-types grown and an increase in pesticide use (Brennan 1991, Burger 2001).

Although the indirect effects of pesticides on bobwhite and other farmland birds in North America are poorly understood (Brennan 1991, Freemark and Boutin 1995), research in Great Britain has shown that pesticides disrupt the food chains of chicks by reducing the availability of key invertebrate species, either by direct kill (insecticides) or through removal of host plants that support phytophagous species (herbicides) (Sotherton and Robertson 1990, Boatman *et al.* 2004). This disruption has been shown to reduce grey partridge chick survival (Potts 1986). While the degree to which pesticides affect the abundance of invertebrates in cropped fields is dependent on many factors, (including chemical efficacy, dosage and timing of application, and dispersal characteristics of a species), their use has been shown to diminish the foraging value of cropped fields for insectivorous farmland birds, not just over one growing season but also long-term (Aebischer and Potts 1990, Donald 1998, Rands 1985, Chiverton and Sotherton 1991, Moreby and Southway 1999).

Since the early 1960's, there has been a vast increase in the use of pesticides in the United States (Donaldson *et al.* 2002). Despite insecticide usage having halved over the last 20 years, the number of insecticide applications per hectare has continued to remain high, particularly for cotton, *Gossypium hirsutum,* crops (Economic Research Service/United States Department of Agriculture (ERS/USDA), http://www.ers.usda.gov). Consequently, because it is recognized from a bird-food resources standpoint that application frequency is a better measure of environmental impact (Robinson and Sutherland 2002), the foraging value of cotton fields for bobwhite chicks is much reduced.

In 1995, the first genetically modified (GM) crops became commercially available in the United States. Despite much debate over the possible ecological effects this new technology may cause, particularly in Europe (Beringer 2000), farmers in the United States have rapidly integrated GM crops into their farming systems (Figure 6.1). In Georgia, GM cotton varieties accounted for 93% (73% nationally) of the total cotton area planted in 2003 (ERS/USDA statistics). The GM cotton varieties currently available in the United States have been biologically engineered to be either tolerant to the herbicide Glyphosate (HTGM), insect-resistant (IRGM) or both, often termed 'stacked' (SGM).

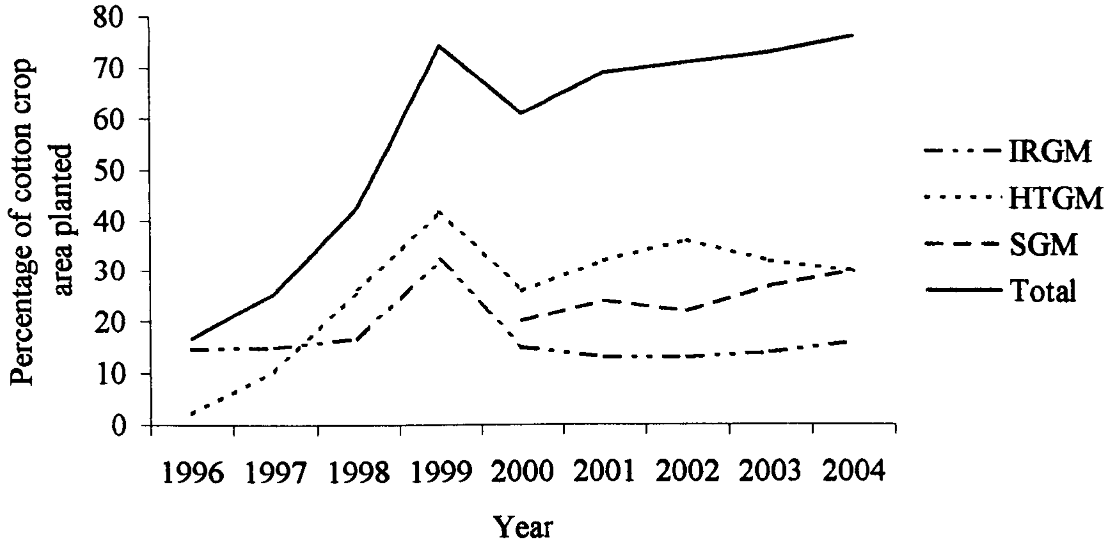


Figure 6.1. Percentage of cotton crop area planted to HTGM, IRGM, and SGM varieties in surveyed states in the United States, 1996-2004. SGM were varieties not commercially available until 2000. ERS/USDA statistics at http://www.ers.usda.gov.

IRGM cotton varieties, introduced commercially in 1996, which accounted for 61% (including SGM varieties) of the cotton area in Georgia in 2003 (ERS/USDA statistics), express the Cry1Ac gene derived from the bacterium *Bacillus thuringiensis* var. *kurstaki* (*Bt*) (Benedict and Altman 2001). GM cotton plants expressing this gene produce proteins that are toxic to Lepidopteran pests such as the pink bollworm, *Pectinophora gossypiella*, tobacco budworm, *Heliothis virescens*, and to a lesser degree the cotton bollworm, *Helicoverpa zea*, that feed on them. These Lepidopteran species are major economic pests of cotton crops and have traditionally been controlled by the use of high quantities of insecticides, often a non-target specific pyrethroid or organophosphate compound (Benedict and Altman 2001). Consequently, it has traditionally been difficult to implement Integrated Pest Management (IPM) cotton production systems because of a lack of tools to control target pests without also disrupting beneficial populations (Fitt 2000). By reducing the need for applying insecticides to control Lepidopteran pests, cotton varieties containing the *Bt* gene may provide better foraging habitat for bobwhite chicks compared with other cotton varieties without it.

Having identified the most important invertebrates in the diet of bobwhite chicks in Chapters IV and V, this information was then used in this field-scale trial to examine how crop-management differences between SGM and HTGM cotton varieties affect the abundance of bobwhite chick-food invertebrates in cropped fields.

2.0 METHODS

2.1 Study site

This study was conducted on Woods Farm, a 250 ha farm situated in Laurens County, central Georgia, United States. The farm was located in the centre of the farmland study site described in Chapter II. The study farm consisted of cropped fields, primarily cotton, peanuts, soybeans, corn, and pasture, interspersed by hedgerows, roads, hardwood drains, planted pine stands, and scrubland (Table 2.1). Three fields that were used in both years of the study had 6m grass strips around their perimeters, as the farm was a participant of the Bobwhite Quail Initiative (BQI) agri-environmental scheme (Georgia Department of Natural Resources 1999).

2.2 Experimental design

Using a randomized block design, with each field representing an individual block, 5 and 14 cotton fields in 2002 and 2003 respectively were divided in two. Fields ranged from five to 18.5 ha ($\bar{x}$ = 10.7 ha) in size, typical of the area. Availability of fields for this study was determined by crop rotation on the farm. Although farm management practices primarily dictated how fields were divided, every effort was made to split the fields so each half-field was similar in size and the surrounding habitat was the same. In each field, one half-field was planted with HTGM cotton (Roundup-Ready®, Monsanto, Inc., Missouri) and the other with SGM cotton (Bollgard® and Roundup-Ready®, Monsanto, Inc., Missouri). The SGM cotton used in both years of the study contained the Cry1Ac transgene. To reflect the current use of cotton varieties in Georgia, 79% of which were herbicide-tolerant (including SGM) in 2003 (ERS/USDA statistics), both treatments (crops) used in this study exhibited the herbicide-tolerant trait. Treatments were randomly assigned to each field-half. Treatments in those fields that were used in both years were switched in the second year. The farmer was asked to complete a comprehensive crop management diary during each year of the study to ensure accurate record keeping.

2.3 Chemical usage

In both 2002 and 2003 a single application of herbicide Glyphosate (Roundup®, Monsanto Inc., Missouri) was applied to both cotton varieties in all fields (Tables 6.1 and 6.2). As a result of limited pest pressure, insecticide use in 2002 was very low, with only the HTGM cotton in one trial field receiving an application of Zeta-cypermethrin (Fury®, FMC Corporation, Pennsylvania) to control bollworms. In 2003, both cotton varieties in 13 fields were sprayed with Dicrotophos (Bidrin®, Shell Chemical Company, Texas) to primarily control southern green stink bugs, *Nezara viridula*. In addition, the HTGM cotton in nine fields was sprayed once with Cypermethrin (Ammo®, United Agri Products, Inc., Colorado) due to bollworm pressure.

Table 6.1. Summary of pesticide applications to half-fields of HTGM and SGM cotton during 2002 and 2003, Georgia, United States. The data were taken from crop management diaries given to the farmer to complete.

Date	Cotton Variety	Field number/s	Chemical use	
			Class	Common Name
2002				
Week 19	Cotton sown			
Week 21-23	Both	1-5	Herbicide	Glyphosate
Week 34	HTGM	3	Insecticide	Zeta-cypermethrin
2003				
Week 18-20	Cotton sown			
Week 21-23	Both	1-14	Herbicide	Glyphosate
Week 32-33	Both	1,2,4,5,6,7,8,12, 13,14	Insecticide	Dicrotophos
Week 34	HTGM	1,2,4,5,6,7,8,12, 13	Insecticide	Cypermethrin
Week 37	Both	9,3,10	Insecticide	Dicrotophos

Table 6.2. Mean number of pesticide applications to half-fields of HTGM and SGM cotton during 2002 and 2003, Georgia, United States. The data were taken from crop management diaries given to the farmer to complete.

Pesticide	Year			
	2002[a]		2003[b]	
	HTGM	SGM	HTGM	SGM
Herbicide				
Glyphosate	1.00	1.00	1.00	1.00
Total	1.00	1.00	1.00	1.00
Insecticide				
Cypermethrin	0.20	0	0	0
Zeta- cypermethrin	0	0	0.64	0
Dicrotophos	0	0	0.93	0.93
Total	0.20	0	1.57	0.93

[a] Number of fields (n) = 5

[b] Number of fields (n) = 14

2.4 Invertebrate abundance

In July, August and September, the middle to late parts of the bobwhite breeding season (Brennan 1999), invertebrate samples were taken to measure invertebrate abundance in each half-field. For each sampling period, sample points were determined by dividing a field edge into approximately 3 equal lengths and then within each third, randomly placing a 12m transect along the edge (<12m from the field edge) and in the centre of the half-field (>12m from the field edge). Six subsamples were therefore taken from each half-field during each sampling period. Invertebrate abundance was assessed in the 'edge' and 'centre' of fields because gamebird chick-food invertebrate abundance can vary between these locations (Green 1984). To avoid the effects of pesticide drift and reduce problems associated with invertebrate-movement between treatments, field edge sample points were located along the field edges that were the greatest distance from the line of division between the two treatments. Also, sample points located in the middle of half-fields were located >30 m from the line of division between treatments. Transects were marked out in a random direction at 45° to the crop rows.

Invertebrate samples were collected by holding the intake cone (opening area = 320 cm^2) of a D-Vac® insect suction sampler (D-Vac Company, Ventura, California) (henceforth, D-Vac) 15cm above the ground and walking at a slow constant pace along the transect (Burger *et al.* 1993, Jackson *et al.* 1987). By using this method, as opposed to the commonly used '5×10 second sucks' method (Poulsen *et al.* 1998, Haughton *et al.* 2003) the invertebrates that would be available to a foraging chick were primarily sampled and not those that were on canopies of tall plants. Furthermore, due to the height and structure of cotton crops, it would have been difficult to take samples in a consistent fashion using the other method (D. Butler, Personal Observation). Invertebrate samples were only taken during fine weather and when vegetation and leaf litter were dry to the touch. Labeled samples were then placed in an airtight box containing naphthalene mothballs for transit from the field to the laboratory where they were transferred to a freezer for storage.

Thawed invertebrates were systematically separated from plant residues and soil particles in each sample. Invertebrates were then identified under a binocular microscope (10-40× magnification), and, using the chick-dietary data presented in Chapter V, pooled into seven groups for analysis; 1) Araneae (including Opilionidae), 2) Orthoptera, 3) Hemiptera 4) Coleoptera (includes Carabidae adults and larvae, Curculionidae, and Chrysomelidae adults and larvae), 5) Formicidae, 6) Total Chick Foods (includes groups 1-5 pooled), 7) Total Invertebrates (includes all invertebrates identified in suction net samples). The invertebrates included in the Total Chick Foods group collectively accounted for over 80% of the invertebrates in the diet of bobwhite chicks on farmland in this region of Georgia (Table 5.3).

2.5 Statistical analysis

Data from 2002 and 2003 were analysed separately because not all fields were sampled in both years. Furthermore, pesticide use varied considerably between years. To normalise distribution, all data were $\log_{10}(n + 1)$ transformed prior to analysis. Initially, analyses were based on whole-season counts per treatment. To examine the effect of distance from field boundary on the abundance of chick-food invertebrates, counts for each sampling distance from the field boundary, <12 m and >12m, were pooled for each half-field. Data were then analysed using analysis of variance (ANOVA) with treatment and field as independent factors and distance as a repeated measures factor. Field was included in the model as a blocking factor (GLM procedure; SPSS Inc. 1998).

For the invertebrate groups, Hemiptera, Total Chick Foods, and Total Invertebrates, monthly (July, August, and September) differences in half-field counts for each month were analysed using ANOVA with treatment and field as independent factors. As before, field was included in the model as a blocking factor.

3.0 RESULTS

3.1 Whole-season invertebrate counts

In 2002, the abundance of Formicidae ($F_{1,4}$ = 21.53, P = 0.01) and Total Chick Foods ($F_{1,4}$ = 12.74, P = 0.023) were greater in the SGM cotton (Table 6.3). However, when Formicidae were removed from the Total Chick Foods group no treatment effect existed ($F_{1,4}$ = 0.20, P = 0.675). Neither the main effect Distance nor the interaction Treatment × Distance had a significant effect on the abundance of any of the invertebrate groups in 2002.

A greater abundance of Hemiptera ($F_{1,13}$ = 9.37, P = 0.009), Total Chick Foods ($F_{1,13}$ = 14.84, P = 0.002), and Total Invertebrates ($F_{1,13}$ = 6.32, P = 0.026) were found in the SGM cotton than the HTGM cotton in 2003 (Table 6.4). Distance had an effect on the groups Hemiptera ($F_{1,13}$ = 24.49, P = <0.001), Coleoptera ($F_{1,13}$ = 7.09, P = 0.02), and Total Chick Foods ($F_{1,13}$ = 7.09, P = 0.02), with a greater abundance being found in the half-field edges than the centre.

3.2 Monthly invertebrate counts

During 2002, no significant differences in the abundance of the groups Hemiptera, Total Chick Foods and Total Invertebrates were found between cotton varieties in July, August, or September (Figure 6.2). Although in July 2003 no differences were found between cotton varieties, significantly greater numbers of Hemiptera ($F_{1,13}$ = 11.37, P = 0.005), Total Chick Foods ($F_{1,13}$ = 27.62, P = 0.000), and Total Invertebrates ($F_{1,13}$ = 14.44, P = 0.002) were found in the SGM cotton in August

(Figure 6.2). In September, the abundance of Total Chick Foods remained greater in the SGM cotton ($F_{1,13} = 11.57$, $P = 0.005$).

Table 6.3. Whole-season mean counts (±SE) of bobwhite chick-food invertebrates in the edge and centre of half-fields ($n = 5$) planted to SGM and HTGM cotton, Georgia, United States, 2002.

	Araneae[a]		Orthoptera		Hemiptera		Coleoptera[b]		Formicidae		Total Chick Foods[c]		Total Invertebrates[d]	
Sample	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Cotton Type														
Edge														
SGM	12.40	2.86	5.20	1.93	50.60	19.56	8.60	2.98	91.20	12.48	168.00	18.83	283.00	58.41
HTGM	7.40	1.21	4.60	1.69	32.60	7.33	3.80	0.97	67.40	5.73	115.80	13.89	181.80	19.82
Centre														
SGM	10.00	2.19	3.20	0.58	22.60	5.07	9.40	5.12	104.80	12.46	150.00	19.89	221.40	18.86
HTGM	12.20	2.71	3.00	0.63	56.80	17.22	6.60	1.44	63.80	11.71	142.40	29.19	217.20	32.87
Half-field Total														
SGM	22.40	3.26	8.40	1.50	73.20	22.46	18.00	7.67	196.00	17.46	318.00	35.61	504.40	68.31
HTGM	19.60	3.33	7.60	1.29	89.40	16.99	10.40	2.16	131.20	12.02	258.20	27.31	399.00	17.00

[a] Includes Opilionidae.

[b] Includes Carabidae adults and larvae, Curculionidae, Chrysomelidae adults and larvae.

[c] All above groups pooled.

[d] All Invertebrates found in suction net samples.

Table 6.4. Whole-season mean counts (±SE) of bobwhite chick-food invertebrates in the edge and centre of half-fields (n = 14) planted to SGM and HTGM cotton, Georgia, United States, 2003.

	Araneae[a]		Orthoptera		Hemiptera		Coleoptera[b]		Formicidae		Total Chick Foods[c]		Total Invertebrates[d]	
Sample	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Cotton Type														
Edge														
SGM	7.57	1.04	7.93	1.55	66.43	9.24	3.36	0.73	49.72	6.57	135.00	12.33	216.57	13.96
HTGM	6.22	0.75	5.29	1.02	54.00	5.26	3.29	0.46	35.14	5.62	103.94	8.11	184.21	9.16
Centre														
SGM	8.00	1.29	6.64	1.01	51.29	6.08	1.86	0.53	48.07	5.26	115.86	10.06	205.29	16.37
HTGM	6.57	1.15	4.14	0.71	37.07	4.27	1.93	0.45	40.50	5.55	90.21	8.11	182.71	12.73
Half-field Total														
SGM	15.57	2.11	14.57	2.23	117.72	14.19	5.22	0.94	97.79	10.17	250.86	20.26	421.86	28.06
HTGM	12.79	1.66	9.43	1.57	91.07	7.84	5.22	0.64	75.64	9.77	194.15	13.42	366.93	18.92

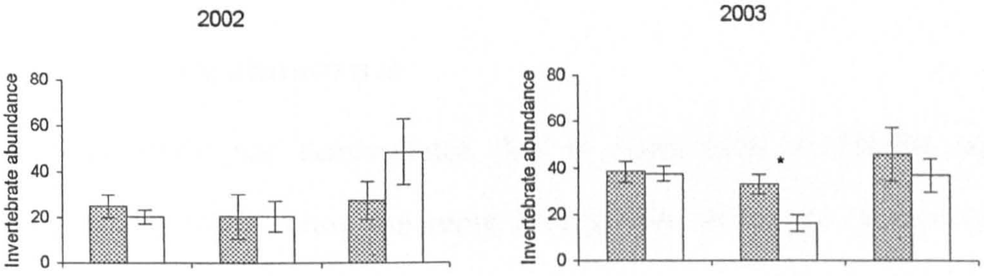
[a] Includes Opilionidae.

[b] Includes Carabidae adults and larvae, Curculionidae, Chrysomelidae adults and larvae.

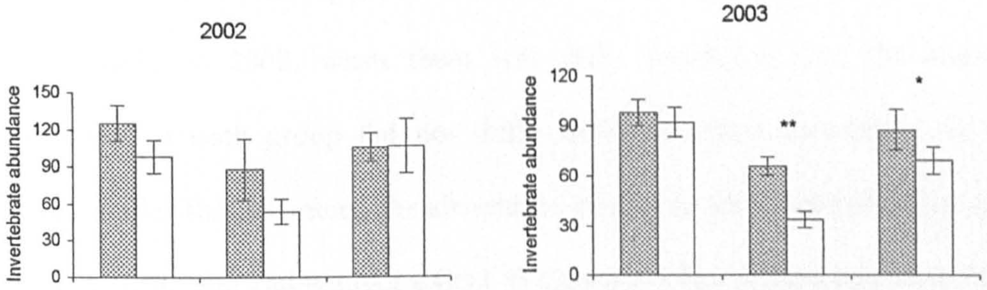
[c] All above groups pooled.

[d] All Invertebrates found in suction net samples.

Hemiptera



Total Chick Foods



Total Invertebrates

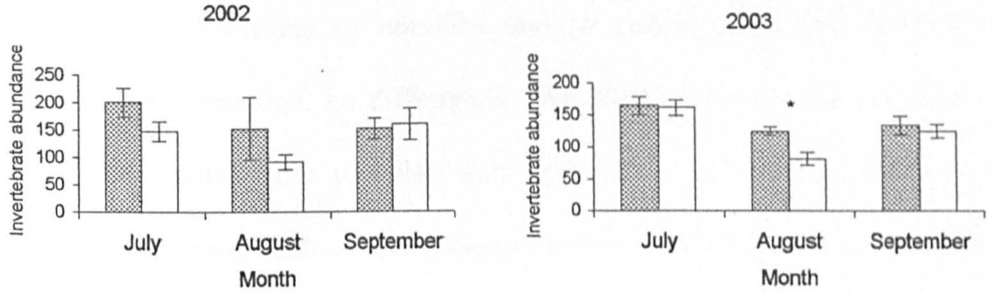


Figure 6.2. Mean monthly (July, August, and September) abundance of the group's Hemiptera, Total Chick Foods, and Total Invertebrates in SGM cotton (solid) and HTGM cotton (clear). Samples collected using an insect suction sampler in half-field plots (2002: *n* = 5; 2003: *n* = 14) on a farm in Georgia, United States, 2002 and 2003. *P = <0.005, **P = <0.001.

4.0 DISCUSSION

4.1 Invertebrate abundance

This study has demonstrated that in comparison to HTGM cotton, the management of SGM cotton can result in a greater abundance of bobwhite chick-invertebrate prey. In addition, because the invertebrate groups studied here are also important in the diet of chicks of other farmland birds (Wilson *et al.* 1999), SGM cotton could provide richer breeding season foraging habitat for other species as well.

Broadly in 2002, when there was little insecticide use, the abundance of invertebrates in each group did not differ between cotton varieties. As shown in previous studies that examined the abundance of non-target invertebrates in varieties of cotton and corn, with and without a Cry1 *Bt* transgene, few differences were found when little or no insecticide was used (Al-Deeb *et al.* 2001, Wold *et al.* 2001, Jasinski *et al.* 2003). In a study conducted in China that examined the abundance of non-target invertebrates within plots of non-GM and *Bt* cotton, with and without insecticide treatments when required, no differences were found between the non-GM cotton and the *Bt* cotton, when both varieties were sprayed or not sprayed (Men *et al.* 2003). However, when insecticides were sprayed on the non-GM cotton and not the *Bt* cotton, and *vice versa*, significantly greater numbers of non-target invertebrates were found in the unsprayed variety in two of the three years of the study.

In August 2003, when pyrethroid was applied to the HTGM cotton, 2.02, 1.95, and 1.53 times more Hemiptera, Total Chick Foods and Total Invertebrates respectively were found in the SGM cotton. Although in September, the numbers of Hemiptera and Total Invertebrates in the HTGM and SGM cotton did not differ, the abundance of Total

Chick Foods was still greater in the SGM cotton, thereby providing improved foraging habitat for bobwhite broods during the middle and late parts of the breeding season (Brennan 1999). A greater whole-season abundance of the groups Hemiptera, Coleoptera and Total Chick Foods was found in the field-edges where gamebird broods prefer to forage (Green 1984).

It is probable that spraying a broad-spectrum organophosphate to control southern green stink bugs in early August 2003 much reduced the abundance of beneficials within both cotton varieties (Inglesfield 1989). This then lead to a classic insecticide-induced outbreak of another pest species. With a reduction in natural enemies, such as minute pirate bugs, *Orius insidiosus*, big-eyed bugs, *Geocoris punctipes*, and ladybird beetles, *Coccinellidae spp*, the economic threshold level of the bollworm/tobacco budworm complex in the HTGM cotton was reached 1-2 weeks after applying the organophosphate. This cyclic insecticide-induced phenomenon is common in cotton production systems and can be repeated a number of times during the growing season, resulting in a high number of insecticide applications (Benedict and Altman 2001). The growing of *Bt* transgenic cotton could interrupt this cycle, as shown in this study, or if bollworms/budworms are the primary pests, which is often the case, reduce the possibility of initiating the insecticide-induced series of events that reduces the abundance of non-target invertebrates.

The short-term negative effects of organophosphate insecticides on densities of non-target invertebrates within non-GM agro-ecosystems have been shown in a number of studies (Vickerman and Sunderland 1977, Cole and Wilkinson 1985, Powell *et al.* 1985). For example, in areas of winter wheat that had been sprayed at the beginning of July with a single application of Dimethoate or left untreated, Vickerman and

Sunderland (1977) reported that the numbers of non-target invertebrates were reduced by 85% in the sprayed areas and after six weeks had only recovered to 40% of that in the control area. It is therefore important that farmers make use of target specific insecticide compounds that conserve non-target species in *Bt* cotton fields.

Although not examined in this study, a decrease in the use of insecticides will also reduce the possibility of pesticide drift that can deleteriously affect non-target invertebrates in adjacent non-cropped areas. In addition to these habitats being important to non-target invertebrates, such as butterflies, which are particularly sensitive to pyrethroid compounds (Çilgi and Jepson 1995), they are also utilized by gamebird broods (Hanson and Progulske 1973, Hill 1985, Stinnett and Klebenow 1986, Taylor *et al.* 1999, Cook 2005) and other farmland birds (Rodenhouse and Best 1994, Brickle *et al.* 2000, Morris *et al.* 2001) during the breeding season, and can be an important source of chick-food invertebrates (Hill 1985, Brickle *et al.* 2000). Consequently, many agro-environmental schemes designed to improve farmland bird habitat in the United States, such as the BQI and the North American Bird Conservation Initiative (NABCI) (Burger 2001) now provide payments for farmers to manage non-cropped areas sympathetically for bird species.

4.2 Study design

By conducting a field-scale study, only the response of invertebrates from the management of the different cotton varieties by a single farmer was examined. However, insecticide use data from previous studies conducted across the United Sates indicate that the crop management (insecticide use) differences seen in this study are typical (Edge *et al.* 2001). Furthermore, by conducting the study on a farm where GMHT cotton has been grown since it was introduced commercially, the farmers' experience from managing GM crops would aid in appropriate crop management decisions being made. Although it would be unrealistic to expect all trials to be on, or even near the size of the Farm Scale Evaluations (FSE) project in Great Britain (Firbank *et al.* 2003), a farm-scale study should now be conducted to examine between farm SGM cotton management differences and their subsequent effects on chick-prey abundance.

In the FSE project conducted in Great Britain, the invertebrate response to the management of 'conventional' non-GM varieties was compared to those of HTGM varieties (Firbank *et al.* 2003). While in Great Britain it is still appropriate to use 'conventional' as a synonym for a farming system that incorporates non-GM crops, in many areas of the United States the use of GM crops has now become conventional practice. Therefore, this study compared the response of bobwhite chick-food invertebrates to the management of the two most widely grown cotton varieties in the United States, SGM and HTGM.

It would be inappropriate to interpret the results of this study as showing that IRGM cotton could also harbor a greater abundance of bobwhite chick-food invertebrates in comparison to HTGM cotton. With the absence of the herbicide tolerance trait a farmer would employ a different herbicide regime. This difference in weed management may therefore lead to a different invertebrate-response, although few differences were found when the management of HTGM and non-GM crops was compared in the FSE study (Haughton *et al.* 2003). Regardless, the weed-management flexibility provided by HTGM crops may aid farmers in employing more environmentally beneficial production techniques such as conservation tillage. This would further enhance the value of cotton to farmland birds and other fauna by providing nesting cover (Minser and Dimmick 1988, Lokemoen and Beiser 1997) and further increasing crop invertebrate abundance (Cederbaum *et al.* 2004).

Although research into the ecological effects arising from the management of GM crops is still in its infancy, studies such as this are increasing our understanding of this complex issue. However, as pesticides have shown, fully understanding the wider ecological consequences of introducing a new technology into farming systems is likely to take much research in the form of both short-term studies and long-term monitoring projects. The use of mathematical models, such as that developed by Watkinson *et al.* (2000) to examine the possible effects of the management of HTGM crops on the availability of weed seeds and the subsequent impact on skylark, *Alauda arvensis*, field use in Great Britain, will also be important in allowing ecologists to explore future scenarios and stimulate debate. Data from field studies like this, allows such models to be continually refined (Sutherland and Watkinson 2001).

Although this study demonstrates that in comparison to HTGM cotton, the management of SGM cotton can lead to a greater abundance of important bobwhite chick-food invertebrates in the crop, this technology should not be seen as a quick fix to increasing the value of cotton fields for farmland wildlife. Instead, these crops should be viewed as an integral part of an IPM system that also incorporates the use of beneficial insects, selective pesticides and other agri-environmental management prescriptions.

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CHAPTER VII

DISCUSSION

1.0 ECOLOGICAL IMPLICATIONS

Although dietary examinations have been infrequently conducted on most North American bird species (Rosenberg and Cooper 1990), this is particularly true for northern bobwhite, *Colinus virginianus,* (henceforth, bobwhite). Despite being one of the most studied gamebird species in the world (Brennan 1993), few studies have examined the diet of bobwhite, particularly during the first two weeks of life (Jackson *et al.* 1987). Rosenberg and Cooper (1990) suggested that a fear of the technical knowledge required to analyse diet samples was a primary reason for why more avian dietary studies had not been conducted. However, as demonstrated in this study, the use of faecal analysis could provide inexperienced researchers with an accurate method for examining large numbers of diet samples. Importantly, this technique also allowed diet samples to be collected from broods in an area where bobwhite populations were low. Because this non-invasive technique does not impact on populations, the diet of a bird species can therefore be examined across its entire geographic range, regardless of population status.

The differences in the diet of bobwhite chicks on plantations and farmland found in this study, underlines the importance of examining geographic variation in bird diets. Because most avian dietary studies in the United States have only collected samples from a single area, it is unknown how their diets change across their geographical range (Rosenberg and Cooper 1990). Consequently, researchers examining food-supply of bird species, including bobwhite, can often only make inferences about the foraging-value of habitats on one landscape based on dietary data from another (Burger *et al.* 1993, Manley *et al.* 1994, Taylor 1996). This, however, assumes that food availability is constant across habitat types, which, due to environmental factors such as vegetation structure, is unlikely (Hutto 1990). It is hoped that this study will therefore stimulate further dietary studies on bobwhite broods so that eventually a detailed picture of how chick-diet varies across the bobwhites' geographic range is obtained. Such a database would also be extremely useful to biologists studying the foraging ecology of other avian species in the United States.

Because of the complex nature of avian foraging ecology, this study is only the first step of many that will be required to fully understand all the factors and relationships that influence the diet of bobwhite chicks. In particular, future dietary studies should examine the indirect effects of weather and predation. As found in other bird species, these factors may be particularly influential on the diet of bobwhite chicks (Erikstad and Spidsø 1982, Brickle and Harper 1999, Potts 1986). Because both weather and predation risk are believed to influence a bird's habitat choice (Forrester *et al.* 1998, Kopp *et al.* 1998, Evans 2004), the selection of foraging-habitats by bobwhite broods is unlikely to be exclusively made on the basis of food-supply. It is therefore likely that adult bobwhite guide their broods to appropriate habitats by constantly managing a risk trade-off, particularly between predation and starvation. By doing this, the broods' foraging efficiency may be reduced by foregoing habitats that offer high availabilities of important prey items. Because of the much lower levels of brood-rearing habitat management and predator control on farms than on plantations in the southeastern United States (Personal Observation), predation pressure levels on bobwhite broods may differ between these two landscapes. Consequently, predator pressure may force broods on farmland to forego invertebrate-rich habitats more frequently than broods on plantations. This may partially explain why in this study a greater proportion of 'poorer' prey items were found in the diet of farmland chicks (Chapter V, Table 5.4).

The innate ability of bobwhite chicks to locate and select prey-items, as demonstrated by the human-imprinted chicks in Chapter IV, may be fundamental in the management of the predation and starvation risk trade-off in bobwhite broods. Once the adult has guided its chicks to a habitat patch where it deems predation risk acceptable, the innate ability of chicks to forage without the guidance of the parent prevents the adult from having to trade-off time between predator vigilance and finding prey-items for the chicks. This adaptation therefore increases the time adult bobwhite can spend scanning for predators and consequently reduces risk of predation. This management of the different risks bobwhite broods face is a much-understudied area of research in game bird chick ecology and, therefore, warrants further examination. The use of human-imprinted chicks may be instrumental in these studies.

Although productivity may be one of the most important factors influencing population change in bobwhite, the life history of chicks is one of the least understood aspects of this species' ecology (Roseberry and Klimstra 1984, Jackson *et al.* 1987, DeVos and Mueller 1993). Because a viable technique for capturing bobwhite chicks has only recently been developed, research into the growth rates of wild chicks has been particularly limited (Smith *et al.* 2003). Although Hammond (2001) used this capture technique to examine chick growth rates on plantations in southern Georgia and northern

Florida, diet samples were not examined. Therefore, this study is the first to show that growth rates of wild bobwhite chicks are related to the invertebrate component of the chick's diet. As shown in chapter V, growth rates of chicks are negatively related the proportion of least selected prey items in the chicks' diet. This result further reinforces the importance of land managers providing bobwhite with brood-rearing habitats rich in important invertebrates. Although survival rates of chicks were not affected by the invertebrate diet of chicks in this study, the results of other gamebird chick survival studies indicate that this may have been due to only examining survival to 10 days (Potts 1986). Because grey partridge, *Perdix perdix*, and ring-necked pheasant, *Phasianus colchicus*, chick survival to 21 days is related to the invertebrate component of the chick's diet (Sotherton *et al.* 1993), future dietary studies should examine bobwhite chick survival to this age.

2.0 MANAGEMENT IMPLICATIONS

It is recognized among gamebird biologists that a sound knowledge of the food requirements of a species is fundamental to the development of habitat prescriptions for improving food-supply within its habitats (Stoddard 1931, Gullion 1966, Sotherton 2000). The work of The Game Conservancy Trust on grey partridge chicks in Great Britain provides an excellent example of this, with the results of detailed dietary studies forming the foundation for the development of habitat management prescriptions that can vastly increase the densities of important chick-prey invertebrates within brood-rearing areas (Sotherton *et al.* 1993). Although biologists in the United States have also used dietary data to help formulate habitat prescriptions for bobwhite broods, the scale and detail of the dietary studies from which these data were taken, was low. In addition, because no published studies have examined the diet of wild bobwhite chicks on farmland, the development and evaluation of prescriptions for this landscape have been based on dietary data from chicks on plantations or other non-agricultural habitats. Consequently, current management practices may not provide optimal habitat for key bobwhite chick-prey invertebrates.

2.1 Agricultural landscapes

2.1.1 Agri-environmental schemes

To maintain adequate stocks for shooting, plantations in the southeastern United States have been highly managed for bobwhite for many years (Stoddard 1931). In fact, many of the habitat management prescriptions used today are similar to those described by Stoddard (1931) over 70 years ago. By contrast, because the production of crops or livestock is the primary concern of farmers, traditionally little time and money was spent on improving habitats on farmland for the benefit of bobwhite or other wildlife. However, in response to the dramatic decline of bobwhite populations on farmland in the southeastern United States, two states within this region, North Carolina and Georgia, have recently introduced specific agri-environmental schemes to help farmers create and maintain bobwhite habitat through technical and financial assistance (Burger 2001).

In Georgia, many of the habitat prescriptions available within the Bobwhite Quail Initiative (BQI) agri-environmental scheme have been primarily designed to increase the amount of insect-rich habitats available to bobwhite broods (Georgia Department of Natural Resources 1999). These include establishing herbaceous field borders (Plate 2.6), allowing weeds to establish in the corners of centre-pivot irrigated fields, and leaving fields uncropped. Although this study was not designed to examine the effects of BQI prescriptions on the diet and survival of wild bobwhite chicks, the results of Chapter V in this study, coupled with those of a study examining brood-habitat use on the same farmland (Cook 2004), suggest they may be positive. While Cook (2004) reported that bobwhite broods positively selected for BQI habitats, the results of this study revealed that the invertebrate-diet of chicks on these farms consisted of a high proportion of important prey items, particularly Hemiptera and Coleoptera, and that chick survival was similar to that found on the highly managed bobwhite shooting plantations. It therefore appears, that chick survival can be high on farmland that has been enhanced by brood-rearing habitat prescriptions due to the increased supply of important chick-prey items. If this is the case, it would mirror the findings of similar British studies, where grey partridge chick survival rates were much improved by establishing insect-rich Conservation Headlands around cereal fields (Sotherton *et al.* 1993). A study specifically designed at examining the diet and survival of bobwhite chicks on farms with and without brood-rearing habitat enhancement should now be conducted.

Unfortunately, due to the lack of historical survival data for bobwhite chicks on farmland, it is unknown what chick survival rate is required to maintain population stability on this landscape. On farmland in Great Britain, Aebischer and Ewald (2004) calculated that a chick survival rate of 35% to 6 weeks was required to maintain grey partridge populations from one year to the next. They also calculated that at least 4% of arable area would need to be insect-rich brood-rearing habitat to achieve this level of survival. Assuming that a BQI field on the Georgia farmland site was square and on average 10.27 ha in size (see page 144), the amount of brood-rearing habitat created by establishing a field around its perimeter was approximately 7.5% of the field area. If this were a field in Great Britain, the Aebischer and Ewald (2004) model would predict that this amount of brood-rearing habitat would produce a grey partridge survival rate of 48%. Interestingly, when the daily bobwhite chick survival rates found in this study (Table 5.7) were used to estimate chick survival to 6 weeks, the mean survival rate was a comparable 41%.

To achieve this level of chick survival across the whole county in which the farmland study site was situated, approximately 600 ha of a total of 37,500 ha of harvested cropland in Laurans County would need to be established as BQI brood-rearing habitat. At a cost of $150/ha/year in incentive payments to farmers, this BQI habitat prescription in one county alone, would cost the Georgia Department of Natural Resources $90,000/ year (www.georgiawildlife.dnr.state.ga.us). This is unlikely to be financially sustainable. However, a high bobwhite chick survival rate may still be achieved if a lower percentage of field area were established to BQI habitat. If BQI field borders were only established on three sides of each field, the amount of insect-rich brood rearing habitat would be 5.7% of arable area, saving approximately $22,500/ year in Laurans County alone. Using the Aebischer and Ewald (2004) grey partridge chick survival model this amount of BQI brood-rearing habitat would still yield a bobwhite chick-survival rate of 41% to 6 weeks old, 6% above the level required for population stability in grey partridge. Unfortunately, however, only 2% of arable land in western Laurans County is currently managed under the BQI scheme (Cook 2004), which, according to the Aebischer and Ewald (2004) model, would only produce a chick survival rate of 26%. Therefore, while on individual BQI farms bobwhite chick survival rates would seem to be above that required to maintain populations, at a county level, bobwhite populations may still be declining due to poor chick survival.

2.1.2 Crop Management

Due to the constraints of financial budgets (www.georgiawildlife.dnr.state.ga.us) and co-operation by farmers (Conover 1998), it is difficult to envisage a sufficient quantity of BQI brood-rearing habitat being established on farmland in Georgia to reverse the dramatic declines of bobwhite populations seen over the last 40 years (Brennan 1991). Consequently, it is therefore imperative that the foraging value of other farmland habitats, particularly cropped fields, is improved. While the conservation and management of weedy marginal areas such as watercourses and hedgerows is important, it is the vast area of arable land in Georgia that, if managed correctly, could significantly increase the amount of foraging habitat available to bobwhite broods.

Prior to the introduction of pesticides and other modern crop production techniques, small, weedy crop fields provided an insect-rich resource for foraging bobwhite broods (Brennan 1991). While it is unlikely that the foraging value of cropped fields will ever return to pre-pesticide levels, some modern crop management techniques are able to improve the invertebrate-richness of arable fields while also reducing production costs (Tillman *et al.* 2004). Conservation tillage is one such technique. By retaining a higher amount of crop residue on the surface of fields than conventional tillage practices (Best 1986), studies have shown that conservation tillage can improve the overall abundance of invertebrates in cropped fields (Basore *et al.* 1987, Cederbaum *et al.* 2004). Furthermore, because conservation tillage alters the vegetation structure of cropped fields within the foraging zone of bobwhite chicks (Castrale 1985), the availability of important chick-prey items is also increased (Palmer 1995). The effect of this on the diet of bobwhite chicks was well demonstrated in a study by Palmer (1995), who reported that the proportion of Coleoptera in the diet of human-imprinted bobwhite chicks after foraging in no-tillage maize, *Zea mays*, fields was nearly double that in the diet of those that had foraged in tilled maize fields.

Encouragingly, the popularity of conservation tillage in the southeastern United States has grown dramatically over the last ten years (Hollis 2005). For example, in 1993 only 6% of cotton was planted into conservation-tilled fields, but by 2004, this had risen to approximately 40% (Hollis 2005). While various factors have probably contributed to this increased use of conservation tillage, the introduction of genetically modified crops is probably one of the most influential reasons for this change. Because herbicide tolerant genetically modified crops allow farmers to effectively control weeds with herbicides during the growing season, cultivations are not required to kill weeds prior to sowing (Firbank and Forcella 2000). Crops can therefore be directly sown into a field leaving the weeds and crop residue on the soil surface intact. It is imperative however, that farmers recognize that no matter how much conservation tillage is able to increase the abundance of chick-prey invertebrates in cropped fields, the use of broad-spectrum insecticides during the growing season can much reduce a fields' foraging value (Inglesfield 1989). As demonstrated in Chapter VI of this study, the bobwhite chick-prey invertebrate abundance of a cotton field can be significantly reduced by the use of insecticides. However, as also found in this study, farmers can reduce the need for insecticidal sprays to control primary insect pests by growing genetically modified insect resistant crops. It would therefore be wise for farmers that practice conservation tillage to plant crops that are both insect resistant and herbicide tolerant in order to preserve the foraging value of these fields for bobwhite and other insectivorous farmland birds.

It is important, therefore, that in addition to establishing herbaceous field borders and other habitat prescriptions available under agri-environmental schemes, farmers should also incorporate such practices as conservation tillage and integrated pest management into their farming systems. Only by adopting this holistic approach to bobwhite-habitat management on farmland will populations be increased on this landscape across the southeastern United States.

2.2 Forested landscapes

As mentioned earlier, in contrast to farmland, habitats on bobwhite shooting plantations in the Southeastern United States have been highly managed for the benefit of bobwhite for many years (Stoddard 1931). Furthermore, because managers recognize the importance of brood-rearing habitat, many habitat management prescriptions typically involve the creation and maintenance of habitats through disking or prescribed burning to attract high densities of invertebrates during the breeding season (Hurst 1972, Manley *et al.* 1994, Parsons *et al.* 2000).

Although land managers recognize that invertebrates are very important in the diet of bobwhite chicks, they are less aware of the factors that determine what invertebrates are eaten by bobwhite chicks in a habitat (Personal Observation). Because much of the literature produced on brood-rearing habitat discusses foraging value in terms of invertebrate abundance rather than availability, the significance of factors such as vegetation structure, invertebrate activity patterns and chick-prey selection in determining the diet of chicks in a habitat are not emphasized to bobwhite managers (DeVos and Mueller 1993, Brennan *et al.* 2000a, Hammond 2001). As a consequence, an area with 'lots of bugs' does not automatically denote quality brood-rearing habitat. For example, although grasshoppers and crickets were found to form between 5-10% of the diet of bobwhite broods on plantations in this study, they were, however, also found to be eaten by chicks much less often relative to their abundance in the field. Therefore, because their size and activity patterns make them difficult for chicks to catch, land managers should be careful not to automatically perceive habitat patches with high numbers of Orthoptera as valuable foraging areas. As Newton (1998) commented, 'no matter the abundance of food in a habitat, if it is unavailable for whatever reason, a bird may starve'.

2.2.1 Prescribed burning

Prescribed burning is one of the cheapest and most effective tools for managing habitats for bobwhite in forested landscapes (Brennan 1991). By killing invasive hardwoods, and thereby preventing a mid-story canopy developing, burning every 1-2 years allows herbaceous ground cover to grow and provide habitat crucial for bobwhite. Although prescribed burning can be conducted all year round, it is typically done during spring (March-May) (Brennan 1994). The period between the end of the bobwhite-shooting season in early March and the start of the nesting season in early May, provides a window in which managers are able to burn. Although managers are often reluctant to burn any later than this because of a perceived risk to nesting bobwhite, there is some evidence that the important chick-prey invertebrates identified in Chapters IV and V in this study may respond better to summer burns (May-June) than those conducted in spring (Brennan *et al.* 2000a). In a small study conducted by Brennan *et al.* (2000a) on Tall Timbers Research Station, burns conducted in May and June produced a greater biomass of important chick-prey invertebrates over the bobwhite-breeding season than those conducted in February and March. Furthermore, in one year of this study, the burns conducted in May and June produced a 'flush' of invertebrates coinciding with the peak of the bobwhite-breeding season in late July. These data, therefore, suggest that managers should at least consider burning some of their land area in early summer as opposed to spring. However, this policy will only be beneficial to bobwhite populations if the resultant increases in chick survival over the whole breeding season outweigh the effects of nest-loss from burning during May and June. This is an important area for future research.

2.2.2 Disking and food plots

Annually disking plots of land to encourage the growth of herbaceous plants has long been recognized as an important bobwhite management tool (Stoddard 1931). The resulting flush of succulent vegetation can harbour high densities of invertebrates during the summer, including many of those identified as important in chapters IV and V of this study (Manley *et al.* 1994, Parsons *et al.* 2000). However, Heteroptera, one of the most selected prey-groups in chapter IV, do not seem to respond favourably to disking (Manley *et al.* 1994, Taylor 1996), particularly when conducted in spring. In one year of a two-year study conducted by Taylor (1996), significantly higher numbers of Heteroptera were found in the non-disked areas than in those disked in spring. Disking in autumn had no effect on any invertebrate group. As invertebrate abundance is inextricably related to the vegetation complex in an area, it is therefore probable that those plant species that are important hosts to Heteropteran species are negatively affected by this management technique.

Rather than simply disking areas of land and allowing weeds to volunteer, wildlife managers often improve the vegetation cover in these disturbed areas by planting crops known to harbour high densities of invertebrates (Stoddard 1931). Research into the abundance of invertebrates in these 'food plots' has shown that different cover crops support different invertebrate species (Burger *et al.* 1993, Brennan *et al.* 2000b). Brennan *et al.* (2000b) reported a greater biomass of Heteroptera in food plots planted with millet, *Panicum spp.*, than in areas that had only been disked in spring. When the food plots were planted with wheat, *Triticum spp.*, however, more Heteroptera were found in the disked plots. For Coleoptera, the reverse was true, with wheat plots having a greater biomass than the disked plots. In a study examining the invertebrate abundance in seven different cover plantings on Conservation Reserve Program fields, red clover, *Trifolium pratense*, harboured the greatest densities of invertebrates, including the key chick-prey groups Heteroptera and Coleoptera (Burger *et al.* 1993). A number of other studies have also demonstrated the ability of clover and other legumes, particularly *Lespedeza spp.*, in hosting high densities of invertebrates (Webb 1963, Jackson *et al.* 1987, Cederbaum *et al.* 2004). Although Stoddard (1931) concluded that simple disking was a more practical, cheaper, and effective management technique on southeastern plantations than food plots, the results of these studies suggest that in order to attract as many important chick-prey invertebrates as possible, bobwhite managers should consider using a combination of both methods within the same field.

Whether on farmland or a plantation, the key to creating quality brood-foraging habitat is to establish habitat that attracts their most important prey items. Although current habitat management techniques have been shown to increase the densities of important chick-prey groups, a fuller understanding of the ecology and habitat requirements of these invertebrates may allow improved prescriptions to be formulated. Detailed research should now be conducted into the ecology and habitat requirements of the most important chick-prey items identified in this study.

3.0 FUTURE RESEARCH

3.1 Topics for future research

It is clear from this research that some invertebrates are of a greater dietary-importance to bobwhite chicks than others. With this knowledge, biologists should now concentrate their efforts on three key areas of research:

1) the ecology and habitat requirements of key chick-prey invertebrates
2) the response of key chick-prey invertebrates to habitat management prescriptions
3) the effect of improving brood-foraging habitats on chick-survival and bobwhite populations

More specifically, bobwhite biologists should consider finding answers to the following biological and management questions:

3.1.1 Biological research

Invertebrate ecology

1). What are the habitat requirements of the important chick-prey invertebrates in agricultural and forested landscapes?

2). How do daily movement patterns of invertebrates affect their availability to chicks in different brood-rearing habitats?

3). Do fire ants, *Solenopis invicta*, reduce the abundance of the important chick-prey invertebrates in different brood-rearing habitats?

4). Within the bobwhites' geographical range, what is the population status of the different key chick-prey invertebrates?

5). What are the nutritional characteristics of the invertebrates eaten by chicks?

6). How do annual changes in weather affect invertebrate abundance and distribution during the breeding season?

7). Is climate change altering the composition of invertebrates within bobwhite brood-rearing habitats?

Bobwhite chick feeding ecology

1). Does the availability of important chick-prey invertebrates influence spatial and temporal distribution of broods?

2). Are daily chick foraging patterns related to the daily activity patterns of important invertebrates?

3). Do chicks select invertebrate prey on the basis of nutritional value? If so, is this an innate or learned behaviour?

4). Does experiencing nutritional stress as a chick, impair adult physiology and breeding performance?

5). Does intra-brood competition for important invertebrates affect breeding success and subsequently influence population levels?

6). Are the long-term declines in bobwhite numbers in different landscapes correlated to any long-term changes in populations of important invertebrates?

3.1.2 Management research

1). How are important chick-prey invertebrates responding to management prescriptions currently established through current federal and state level agri-environmental schemes?

2). How does the timing and frequency of prescribed burning on forested landscapes affect the availability and distribution of important chick-prey invertebrates?

3). How does the timing and frequency of disking on forested landscapes affect the availability and distribution of important chick-prey invertebrates?

4). Does conservation tillage increase the availability of important chick-prey invertebrates in arable fields?

5). How are long-term invertebrate populations responding to the introduction of Genetically Modified crop varieties?

4.0 CONCLUSION

This study is the first to demonstrate that fitness of wild bobwhite chicks is affected by the invertebrate component of the chick's diet. As the proportion of least selected prey items in the diet of chick's increased, the lower their growth rates became. Furthermore, the results of this study suggest that bobwhite chicks have an innate ability to select against these invertebrate groups. The results of this study now provide bobwhite biologists with a good starting point on which to design and evaluate brood-rearing habitat management prescriptions, both on agricultural and farmland landscapes. A comprehensive knowledge of the food requirements of bobwhite chicks will now allow biologists to gain a detailed understanding of how short and long-term changes in ecosystems, particularly from anthropogenic activities, affect bobwhite chick-food supply and ultimately population stability.

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