

ABSTRACT

BUTLER, ERIC MICHAEL. Habitat Selection and Anti-Predator Responses of Acridid Grasshoppers. (Under the direction of Marianne Niedzlek-Feaver and Harold Heatwole.)

Most prey species use a variety of defenses to prevent their capture by predators. Habitat can have both direct effects on the effectiveness of these defenses by providing refuges, the backgrounds against which prey species are camouflaged, and, indirectly, by altering exposure to the predator community of the broader region. Grasshoppers are found in multi-species assemblages in geographically-proximate micro-habitats and are subject to a number of predators from a wide variety of taxa. The main defenses of most grasshoppers are the opposed strategies of hiding and fleeing. More structurally-complex habitats should favor hiding while more open habitats should favor fleeing. To test this hypothesis I evaluated the micro-habitat preferences of nine species of sympatric grasshoppers found in fields at Raleigh, North Carolina. While several species had distinct preferences for habitats with taller or shorter vegetation, the presence or absence of vegetative cover was an important factor for nearly all species. Escape behavior was also recorded for all nine species. Species-specific differences were seen in flight-initiation distances and flight distances. Camouflage was evaluated using a computer program in which humans tried to locate camouflaged grasshoppers as rapidly as possible. Because any close correlation between camouflage and habitat assumes that camouflage will be lost if it is superseded by other defenses in a given habitat, this assumption was investigated. Twenty-one island-endemic species of birds and mammals that have few to no predators when compared to their closest relatives on the mainland were located. The island-endemic species were not appreciably different from the species found on the mainland when their color patterns were

compared both by eye and by a computerized scoring system. When all results were compared habitat was found to have a strong correlation with escape behavior with species found more often in bare-ground habitats beginning escape attempts when predators were further off and continuing their escape flights for longer. Camouflage was marginally correlated with both bare-ground preference and longer flight-initiation distances, perhaps because camouflage is not always reduced when it ceases to be of primary importance. Of all the traits examined in these studies escape behavior showed the greatest phylogenetic inertia, suggesting that over evolutionary time habitat choice and camouflage may evolve in ways that compensate for, or benefit from, escape behavior.

© Copyright 2011 by Eric Michael Butler

All Rights Reserved

Habitat Selection and Anti-Predator Responses of Acridid Grasshoppers

by
Eric Michael Butler

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Zoology

Raleigh, North Carolina

2012

APPROVED BY:

Dr. Marianne Niedzlek-Feaver
Co-Chair of Advisory Committee

Dr. Harold Heatwole
Co-Chair of Advisory Committee

Dr. Rob Dunn

Dr. Thomas Reiland

BIOGRAPHY

Eric Butler was born in Boston, MA, and spent most of his childhood in Acton, MA. He attended Acton-Boxborough Regional High School and from there went on to obtain a B.S. in Ecology from Juniata College in Huntingdon, PA. During his time at Juniata he worked in Dr. Douglas Glazier's laboratory studying physiological ecology. Knowing that he wished to continue further in his education, Mr. Butler entered the doctoral program at North Carolina State University immediately upon graduation from Juniata. Intrigued by how predators might influence the ecology of their prey he chose to work with the large and accessible grasshopper assemblage in the Raleigh, NC area. As many interesting questions remain unanswered, Mr. Butler plans to continue investigating the relationships between grasshoppers and their predators, especially with regard to escape behavior and camouflage, in his future work.

ACKNOWLEDGMENTS

I would like to thank, firstly, my wife Sharon Butler who has endured my years of long, erratic hours and low pay with great patience and support for my academic goals. Without her dedication and care I would be in a much worse place by now.

I would also like to thank both my family and Sharon's family for their understanding and aid even when my work seemed esoteric at best.

I also wish to thank my committee members, Marianne Niedzlek-Feaver, Harold Heatwole, Rob Dunn, and Tom Reiland, for their support, mentoring, and effort on my behalf. I owe the abilities I have today to their efforts.

Much of the work on this project has taken place at the Lake Wheeler Farm Unit and I thank the staff there for their patience with my research and for consistently finding an unmown field or two on which I could work.

Finally, it would be remiss of me not to thank the doctors and nurses of Duke Oncology without whom I would not have finished this dissertation, or anything else ever again.

TABLE OF CONTENTS

	Page
LIST OF TABLES	vi
LIST OF FIGURES	viii
Chapter One..... GENERAL INTRODUCTION	1
Chapter Two..... MICROHABITAT PREFERENCES OF NINE SPECIES OF ACRIDID GRASSHOPPER.....	13
2.1 Introduction	14
2.2 Methods	16
2.3 Results	22
2.4 Discussion	25
2.5 Literature Cited	30
Chapter Three.... SPECIES-SPECIFIC ESCAPE BEHAVIOR IN GRASSHOPPERS	43
3.1 Introduction	44
3.2 Methods	45
3.3 Results	52
3.4 Discussion	58
3.5 Literature Cited	61
Chapter Four..... A QUANTATIVE INVESTIGATION OF GRASSHOPPER CAMOUFLAGE	68
4.1 Introduction	69
4.2 Methods	71
4.3 Results	76
4.4 Discussion	79
4.5 Literature Cited	84
Chapter Five DOES CRYPSIS HAVE AN EVOLUTIONARY COST? AN INVESTIGATION USING PREDATOR-FREE ISLAND SPECIES	91
5.1 Introduction	92
5.2 Methods	96
5.3 Results	105
5.4 Discussion	107
5.5 Literature Cited	109

Chapter Six..... CONCLUSIONS	119
6.1 Introduction	120
6.2 Methods	122
6.3 Results	123
6.4 Discussion	126
6.5 Literature Cited	131

LIST OF TABLES

	Page
 CHAPTER TWO	
Table 2.1. Numbers of each species of grasshopper observed on manipulated plots	37
Table 2.2. P-values for vegetation-height variables as predictors of grasshopper abundance on plots.....	37
Table 2.3. R-squared values for correlations between grasshopper abundance and vegetation-height measurements	38
Table 2.4. P-values for significant correlations between per-plot abundance of grasshoppers and forb cover	38
Table 2.5. P-values for significant correlations between per-plot abundance of grasshoppers and the patchiness of habitats	38
Table 2.6. Numbers of grasshoppers observed in each transect.....	39
 CHAPTER THREE	
Table 3.1. Species comparisons for FIDs.....	65
Table 3.2. Species comparisons for flight distances	66
Table 3.3. The FID and flight distances of grasshoppers listed by the average for each species.....	67
 CHAPTER FOUR	
Table 4.1. Color-species comparisons of raw camouflage data.....	88
Table 4.2. Greenness values calculated for grasshoppers and their backgrounds by color-species	89
Table 4.3. Correlations between the greenness of the background and the time it took a user to correctly locate a grasshopper	89
Table 4.4. Residuals from a model predicting the time it took to locate a grasshopper by the greenness difference between the	

grasshopper and the background	90
--------------------------------------	----

CHAPTER FIVE

Table 5.1. Species included in the study described in Chapter Four	115
--	-----

LIST OF FIGURES

	Page
 CHAPTER TWO	
Figure 2.1. The percent of observations made in short and tall plots by species.....	41
Figure 2.2. The percent of observations made on the bare side and covered side of the edge transects by species	42
 CHAPTER SIX	
Figure 6.1. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for FID	134
Figure 6.2. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for flight distance	135
Figure 6.3. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for short-versus-tall vegetation preference	136
Figure 6.4. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for bare-versus-covered habitat preference	137
Figure 6.5. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for camouflage scores	138
Figure 6.6. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for body length.....	139

CHAPTER ONE
GENERAL INTRODUCTION

All species possess some defenses against predators, without which they would be eaten into extinction. However, defenses frequently incur some sort of cost (Dodson, 1984; Ydenberg and Dill, 1986; Benard and Fordyce, 2003; Laurila et al., 2008). In the absence of such costs species should trend towards invincibility, evolving defense after defense. Instead, even well-defended species suffer occasional predation (Joubert, 2006; Pitman et al., 2001; Sweitzer, 1996; Master, 1999). To maximize the value of costly defenses, species should tailor the defenses they use to the predators they face and the habitats they utilize.

Dewitt et al. (1999) suggested four main ways whereby individual defensive traits might relate. Codependent traits are those that are physically linked and therefore always occur together. Complementary traits are those that occur together because each trait becomes much more effective in the presence of its complement. Compensation and cospecialization describe traits that are negatively or positively correlated with one another, respectively. The presence of both compensation and cospecialization in natural environments (Dewitt et al., 1999; Cotton et al., 2004; Mikolajewski & Johansson, 2004; Lakowitz et al., 2008) make predicting trait relationships somewhat difficult. However, cospecialization is effective only in areas where the less-defended phenotypes are not exterminated, which suggests that predation pressure may be important in determining whether compensation or cospecialization should be expected.

While Dewitt et al. (1999) did not provide a term for traits that interfere with one another, such anti-complementary traits do exist. One classic example is camouflage and escape behavior. An individual that flees loses the benefit of camouflage (Broom & Ruxton, 2005) (with a few exceptions, see Brodie [1992] and Forsman and Appelqvist [1998]). A

number of studies on lizards have found that more conspicuous individuals or closely-related species flee from an approaching potential predator at greater distances than do more cryptic individuals or species (Heatwole, 1968; Martin and Lopez, 1999; Martin et al., 2009; Cabido et al., 2009).

This series of studies is focused on antipredator adaptations in nine species of acridid grasshopper, *Schistocerca Americana*, *Dichromorpha viridis* and *Syrbula admirabilis*, *Melanoplus femurrubrum*, *Melanoplus differentialis*, *Dissosteira carolina*, *Chortophaga viridifasciata*, *Spharagemon cristatum*, and *Hippiscus ocelote*, that co-occur in the same fields at Raleigh, North Carolina. Because of the sympatry and relatedness of the subject species, a number of features that are not the focus of this study are consistent between species.

Like most large insects, all nine species are preyed upon by a range of vertebrate and invertebrate predators (Judd, 1899; Giles, 1939; Scott, 1943; Moore & Strickland, 1954; Evans, 1964; Mook & Davies, 1966; Punzo, 1991; Joern & Rudd, 1982). None of these species is believed to be chemically defended beyond the regurgitate most species of grasshopper expel when handled (Sword, 2001). All nine species of grasshopper in this study are also prone to flee under certain conditions and one of them, *Dissosteira carolina*, has been the subject of a study on escape behavior similar to the one I have conducted on all nine species (Cooper, 2006).

The ability of each species to flee varies markedly. In one species, *Dichromorpha viridis*, most individuals are brachypterous. Other species, notably *Schistocerca americana* and *Dissosteira carolina*, are capable flyers. While all nine species are found on some of the

same fields, the microhabitats available in these locations vary from bare ground to tall, thick grass. In a similar manner, the species range from being quite difficult to locate visually to being relatively easy to see. For these reasons this set of species is an appropriate group of model organisms for this investigation.

The first study focused on habitat usage by these grasshoppers. The second study focused on the escape behavior of these grasshoppers. The last two studies focused on camouflage, with the third study quantifying the camouflage of the study species and the fourth study examining a number of species to determine whether camouflage is a costly adaptation.

A number of studies have shown differential habitat usage by various species of grasshoppers (Whelan, 1938; Isely, 1937; Isely, 1938; Friauf, 1953; Joern and Lawlor, 1980; Joern and Lawlor, 1981, Joern, 1982, Capinera et al., 1997; Craig et al., 1999; Squitier and Capinera, 2002). While predator avoidance may drive microhabitat usage in a few species under particular conditions (Schmitz and Suttle, 2001; Stidham and Stidham, 2008), habitat preferences are probably primarily driven by other factors. Despite this, habitat choice affects both the predation regime a species faces and the utility of the tactics it uses to defend itself. Several studies have shown that predatory arthropods are more common in more structurally complex habitats (Balfour and Rypstra, 1998; Brose, 2003) and Russel (1989) suggested that herbivorous arthropods suffer higher mortality from predatory arthropods in ecosystems that have a high plant diversity. However, Leber (1985) found that structural complexity of a habitat lowered predator-induced mortality in a number of prey-species in a

marine environment. In this case the structural complexity of the habitat was believed to provide shelter from larger predators.

Habitat structure is also expected to influence the choice between hiding and fleeing. It is simply much harder to hide in a habitat without cover and a number of studies support the idea that species respond to this by altering their flight responses in response to the amount of cover. Cuadrado et al. (2001) found that chameleons that were perched in more enclosed positions were harder to locate but were also less likely to engage in active escape and defense behavior when approached. Similarly, Amo et al. (2007) showed both that predators were able to detect the lizard *Psammodromus algirus* at longer ranges in more open habitat and that the lizard fled while predators were further away in these habitats. At the species level, Goodman (2009) showed that lizard species found in open habitats tended to have longer limbs and, presumably, higher running speeds. Gutzwiller and Marcum (1997) noted another effect of habitat: predators are also less able to hide in open habitat and are detected and potential prey flee from them earlier.

In this study I have quantified microhabitat choice in relation to cover. Habitat pairs (tall versus short vegetation and vegetated areas versus bare ground) were identified and surveyed for grasshoppers. Each grasshopper's current habitat was noted along with its species. This allowed habitat preference to be expressed as a percent when relating habitat preference to other variables.

Escape behavior was quantified in a manner similar to that of Cooper (2006). Three measures of escape behavior were used: flight-initiation distance (the distance between the model predator and the grasshopper when the grasshopper initiates its escape), the straight-

line flight distance, and the angle between the model predator's approach path and the straight-line flight path of the grasshopper.

Camouflage was also quantified using a system in which human viewers located grasshoppers in a modified picture on a computer screen. The speed with which the viewer located the grasshopper was used to calculate a camouflage score. This is similar to a system used by Fraser et al. (2007) to determine the value of disruptive camouflage. Others studies have demonstrated that at least some grasshopper species gain survival value from camouflage (Isley, 1938; Gillett and Gonta, 1978; Forsman and Appelqvist, 1998). Three of the species observed in this study, *Chortophaga viridifasciata*, *Dichromorpha viridis*, and *Syrbula admirabilis* have multiple color phases which have been shown to be correlated with the average background color of their environment (Otte and Williams, 1972).

Additionally, the body lengths (head to wing tips in most cases, head to abdomen end if that was longer) of fifty specimens of each species were measured to obtain a species average. The average size of a grasshopper is expected to influence the ability of predators, especially invertebrate predators, to subdue it (Whitman and Vincent, 2008). However, as body size becomes larger, vertebrate predators become an increasing problem, presumably because a large grasshopper is worth more effort for a predatory vertebrate (Belovsky et al., 1990).

Finally, in some species it has been suggested that defenses persist after their usefulness has ended (Peckarsky and Penton, 1988; Byers, 1997). If this is the case then one should not expect to see trade-offs in defenses. Instead, some "legacy" defenses will remain whether or not they have immediate utility. I have examined the issue of whether one of the

defenses I have studied, camouflage, persists in the absence of predators by comparing species from islands on which there are no predators large enough to prey upon adults of the species, with the nearest relatives of the species that do experience predation as adults. The other defensive system I have examined, escape behavior, has already been examined in regard to this issue in several taxa (Berger et al., 2001; Blumstein, 2002; Blumstein and Daniel, 2002; Blumstein and Daniel, 2005), although no single pattern has emerged from these studies. In the case of camouflage, Endler's studies (1978, 1983, 1986) show that camouflage can be lost under certain circumstances. However, the expected costs to camouflage are all opportunity costs. In Endler's studies the cost of camouflage was that more brightly-colored male guppies mated more often than did camouflaged ones. Endler (1978) proposed that camouflage must be balanced against thermoregulation and social signaling. Other work has also suggested that coloration can be important for mechanical strength of certain body parts and for protection from UV light (Averill, 1923; Majerus 1998; Goldstein et al., 2004). While these findings certainly suggest that the opportunity costs of camouflage should be sufficient to cause the disappearance of camouflage over evolutionary time when it becomes unnecessary, little work has been done on this topic.

Works Cited

- Amo, L., Lopez, P., & Martin, J. (2007). Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. *Canadian Journal of Zoology*, 85(6), 743-751.
- Averill, C. K. (1923). Black wing tips. *Condor*, 25(2), 57-59.
- Balfour, R. A., & Rypstra, A. L. (1998). The influence of habitat structure on spider density in a no-till soybean agroecosystem. *Journal of Arachnology*, 26, 221-226.

- Belovsky, G. E., Slade, J. B., & Stockhoff, B. A. (1990). Susceptibility to predation for different grasshoppers: An experimental study. *Ecology*, *71*(2), 624-634.
- Benard, M. F., & Fordyce, J. A. (2003). Are induced defenses costly? Consequences of predator-induced defenses in Western toads, *Bufo boreas*. *Ecology*, *84*(1), 68-78.
- Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science*, *291*, 1036-1039.
- Blumstein, D. T. (2002). Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *Journal of Biogeography*, *29*, 685-692.
- Blumstein, D. T., & Daniel, J. C. (2002). Isolation from mammalian predators differentially affects two congeners. *Behavioral Ecology*, *13*, 657-663.
- Blumstein, D. T., & Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proceedings: Biological Sciences*, *272*(1573), 1663-1668.
- Brodie, E. D. I. I. I. (1992). Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. *Evolution*, *46*, 1284-1298.
- Broom, M., & Ruxton, G. D. (2005). You can run — or you can hide: optimal strategies for cryptic prey. *Behavioral Ecology*, *16*, 534-540.
- Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: mediated by vegetation structure or plant diversity? *Oecologia*, *135*, 407-413.
- Byers, J. A. (1997). *American pronghorn: social adaptations and the ghosts of predators past*. Chicago: University Chicago Press.
- Cabido, C., Galan, P., Lopez, P., & Martin, J. (2009). Conspicuousness-dependent antipredatory behavior may counteract coloration differences in Iberian rock lizards. *Behavioral Ecology*, *20*(2), 362-370.
- Capinera, J. L., Scherer, C. W., & Simkins, J. B. (1997). Habitat associations of grasshoppers at the Macarthur Agro-Ecology Research Center, Lake Placid, Florida. *The Florida Entomologist*, *80*(2), 253-261.
- Cooper, W. E. (2006). Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. *Behaviour*, *143*(10), 1201-1218.
- Cotton, P. A., Rundle, S. D., & Smith, K. E. (2004). Trait compensation in marine gastropods: Shell shape, avoidance behavior, and susceptibility to predation. *Ecology*, *85*(6), 1581-1584.

- Craig, D. P., Bock, C. E., Bennett, B. C., & Bock, J. H. (1999). Habitat relationships among grasshoppers (Orthoptera: Acrididae) at the Western limit of the Great Plains in Colorado. *American Midland Naturalist*, 142(2), 314-327.
- Cuadrado, M., Martin, J., & Lopez, P. (2001). Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biological Journal of the Linnean Society*, 72(4), 547-554.
- Dewitt, T. J., Sih, A., & Hucko, J. A. (1999). Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. *Animal Behaviour*, 58(2), 397-407.
- Dodson, S. I. (1984). Predation of *Heterocope septentrionalis* on two species of *Daphnia*: Morphological defenses and their cost. *Ecology*, 65(4), 1249-1257.
- Endler, J.A. (1983). Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, 9, 173-190.
- Endler, John A. (1978). A predator's view of animal color patterns. *Evolutionary Biology*, 11, 319-364.
- Endler, John A. (1986). Convergent and divergent effects of natural selection on color patterns in two fish faunas. *Evolution*, 36, 178-188.
- Evans, F. C. (1964). The food of vesper, field and chipping sparrows nesting in an abandoned field in southeastern Michigan. *American Midland Naturalist*, 72(1), 57-75.
- Forsman, A., & Appelqvist, S. (1998). Visual predators impose correlational selection on prey color pattern and behavior. *Behavioral Ecology*, 9(4), 409-413.
- Fraser, S., Callahan, A., Klassen, D., & Sherratt, T. N. (2007). Empirical tests of the role of disruptive coloration in reducing detectability. *Proceedings of the Royal Society B Biological Sciences*, 274(1615), 1325-1331.
- Friauf, J. J. (1953). An ecological study of the Dermaptera and Orthoptera of the Welaka Area in Northern Florida. *Ecological Monographs*, 23(2), 79-126.
- Giles, L. W. (1939). Fall food habits of the raccoon in central Iowa. *Journal of Mammalogy*, 20(1), 68-70.
- Gillett, S. D., & Gonta, E. (1978). Locust as prey: Factors affecting their vulnerability to predation. *Animal Behaviour*, 26(1), 282-289.

- Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M., & Burt Jr., E. H. (2004). Bacterial degradation of black and white feathers. *The Auk*, 121(3), 656-659.
- Goodman, B. A. (2009). Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. *Journal of Evolutionary Biology*, 22(7), 1535-1544.
- Gutzwiller, K. J., & Marcum, H. A. (1997). Bird reactions to observer clothing color: implications for distance-sampling techniques. *Journal of Wildlife Management*, 61, 935-947.
- Heatwole, H. (1968). Relationship of escape behavior and camouflage in anoline lizards. *Copeia*, 1968, 109-113.
- Isely, F. B. (1937). Seasonal succession, soil relations, numbers, and regional distribution of North-Eastern Texas Acridians. *Ecological Monographs*, 7(3), 317-344.
- Isely, F. B. (1938). The relations of Texas Acrididae to plants and soils. *Ecological Monographs*, 8(4), 551-604.
- Isely, F. B. (1938). Survival value of acridian protective coloration. *Ecology*, 19(3), 370-389.
- Joern, A. (1982). Vegetation structure and microhabitat selection in grasshoppers (Orthoptera, Acrididae). *Southwestern Naturalist*, 27(2), 197-209.
- Joern, A., & Lawlor, L. R. (1980). Food and microhabitat utilization by grasshoppers from arid grasslands: Comparisons with neutral models. *Ecology*, 61(3), 591-599.
- Joern, A., & Lawlor, L. R. (1981). Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos*, 37, 93-104.
- Joern, A., & Rudd, N. T. (1982). Impact of predation by the robber fly *Proctacanthus milbertii* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. *Oecologia*, 55(1), 42-46.
- Joubert, D. (2006). Hunting behaviour of lions (*Panthera leo*) on elephants (*Loxodonta africana*) in the Chobe National Park, Botswana. *African Journal of Ecology*, 44(2), 279-281.
- Judd, S. D. (1899). The efficiency of some protective adaptations in securing insects from birds. *The American Naturalist*, 33(390), 461-484.

- Lakowitz, T., & Bronmark, C Nystrom, P. (2008). Tuning in to multiple predators: conflicting demands for shell morphology in a freshwater snail. *Freshwater Biology*, 53(11), 2184-2191.
- Laurila, A., Lindgren, B., & Laugen, A. T. (2008). Antipredator defenses along a latitudinal gradient in *Rana temporaria*. *Ecology*, 89(5), 1399-1413.
- Leber, K. M. (1985). The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology*, 66, 1951-1964.
- Majerus, M. E. N. (1998). *Melanism* (pp. 28-29). New York: Oxford University Press.
- Martin, J., & Lopez, P. (1999). Nuptial coloration and mate guarding affect escape decisions of male lizards *Psammodromus algirus*. *Ethology*, 105(5), 439-447.
- Martin, J., Luque-Larena, J. J., & Lopez, P. (2009). When to run from an ambush predator: balancing crypsis benefits with costs of fleeing in lizards. *Animal Behaviour*, 78(4), 1011-1018.
- Master, T. L. (1999). Predation by rufous motmot on black-and-green poison dart frog. *Wilson Bulletin*, 111(3), 439-440.
- Mikolajewski, D. J., & Johansson, F. (2004). Morphological and behavioral defenses in dragonfly larvae: trait compensation and cospecialization. *Behavioral Ecology*, 15(4), 614-620.
- Mook, L. J., & Davies, D. M. (1966). European praying mantis (mantis religiosa) as a predator of red-legged grasshopper (*Melanoplus femurrubrum* (de Geer)). *Canadian Entomologist*, 98(9), 913-918.
- Moore, J. E., & Strickland, E. H. (1954). Notes on the food of three species of Alberta amphibians. *American Midland Naturalist*, 52(1), 221-224.
- Otte, D., & Williams, K. (1972). Environmentally induced color dimorphisms in grasshoppers. *Syrbula admirabilis*, *Dichromorpha viridis*, and *Chortophaga viridifasciata*. *Annals of the Entomological Society of America*, 65(5), 1154-1161(8).
- Peckarsky, B. L., & Penton, M. A. (1998). Why do *Ephemerella* nymphs scorpion posture: a “ghost of predation past”? *Oikos*, 53, 185-193.
- Pitman, R. L., Ballance, L. T., Mesnick, S. I., & Chivers, S. J. (2001). Killer whale predation on sperm whales: observations and implications. *Marine Mammal Science*, 17(3), 494-507.

- Punzo, F. (1991). Field and laboratory observations on prey items taken by the wolf spider, *Lycosa lenta* Hentz (Araneae, Lycosidae). *Journal of Arachnology*, 8(8), 261-264.
- Russell, E. P. (1989). Enemies hypothesis: a review of the effect of vegetation diversity on predatory insects and parasitoids. *Environmental Entomology*, 18, 590-599.
- Schmitz, O. J., & Suttle, K. B. (2001). Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, 82(7), 2072-2081.
- Scott, T. G. (1943). Some food coactions of the northern plains red fox. *Ecological Monographs*, 13(4), 427-479.
- Squitier, J. M., & Capinera, J. L. (2002). Habitat associations of Florida grasshoppers (Orthoptera: Acrididae). *The Florida Entomologist*, 85(1), 235-244.
- Stidham, J. A., & Stidham, T. A. (2008). Bull nettle (*Cnidoscolus texanus*) as enemy free space for Orthopterans in Texas, U.S.A. *Entomological News*, 119(1), 102-104.
- Sweitzer, R. A. (1996). Predation or starvation: Consequences of Foraging decisions by porcupines (*Erethizon dorsatum*). *Journal of Mammalogy*, 77, 1068-1077.
- Sword, G. A. (2001). Tasty on the outside, but toxic in the middle: Grasshopper regurgitation and host plant-mediated toxicity to a vertebrate predator. *Oecologia*, 128(3), 416-421.
- Whelan, D. B. (1938). Orthoptera of an Eastern Nebraska prairie. *Journal of the Kansas Entomological Society*, 11(1), 3-6.
- Whitman, D. W., & Vincent, S. (2008). Body size in Orthoptera; Preface. *Journal of Orthoptera Research*, 17(2), 113-114.
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, 16, 229-249.

CHAPTER TWO

MICROHABITAT PREFERENCES OF NINE SPECIES OF ACRIDID GRASSHOPPER

INTRODUCTION

Grasshoppers are important invertebrate herbivores in grassland habitats (Otte, 1981). Numerous studies have shown that grasshopper species are found in association with specific microhabitats (Rehn and Hebard, 1909; Hebard, 1925; Hebard, 1931; Whelan, 1938; Isely, 1937; Isely, 1938; Friauf, 1953; Joern and Lawlor, 1980; Joern and Lawlor, 1981; Joern, 1982, Capinera et al., 1997; Craig et al., 1999; Squitier and Capinera, 2002) but the mechanisms for habitat selection are not always clear. The availability of suitable food, appropriate substrate for oviposition, and temperature profile have all been suggested as essential habitat requirements (Isely, 1938; Clark, 1948; Anderson, 1964; Anderson et al., 1979; Willott 1997). Recently, there have also been studies that indicate that grasshoppers spend time amongst certain plants thereby reducing predation pressure (Schmitz and Suttle, 2001; Stidham and Stidham, 2008).

A significant body of literature has shown that habitat characteristics can be important mediators of predator-prey interactions. Complex habitats may provide prey with refugia that protect them from predators (Leber, 1985; Messina et al., 1997; Clark and Messina, 1998a, 1998b; Lewis and Eby, 2002). Even partial refuges may lower the effectiveness of predators (Gillett and Gonta, 1978; Crowder and Cooper, 1982; Babbitt and Tanner, 1998; Groner and Ayal, 2001), possibly by hindering movement and raising the metabolic costs associated with attacking prey (Glass, 1971; Yang, 2000). Other habitat features can impede or improve the searching ability of predators (Kaiser, 1983; Geitzner and Bernays, 1996; Grevstad and Kleptka, 1992). Conversely, the presence of refuges may limit intraguild predation and increase total predation pressure (Finke and Denno, 2002). Many arthropod predators are found in higher densities within more complex habitats (Hanks and Denno, 1993; Agrawal and Karban, 1997;

Rypstra et al., 1999; Sunderland and Samu, 2000; Brose, 2003, Langellotto and Denno, 2004) and predation by vertebrate predators has been suggested as an explanation for this pattern (Gunnarsson, 1990; Brose, 2003), suggesting that the habitat choice of an invertebrate prey species may also be a choice between predator groups.

Grasshoppers are preyed upon by numerous vertebrate and invertebrate predators (Judd, 1899; Moore and Strickland, 1954; Landry, 1970; Plummer, 1981; Joern and Rudd, 1982; Belovsky and Slade, 1993; Cepek, 2004). The ability of these predators to suppress grasshopper populations varies among studies (Richards and Waloff, 1954; Joern, 1986; Hurd and Eisenberg, 1990; Fowler et al., 1991; Bock et al., 1992; Joern, 1992; Belovsky and Slade, 1993; Beckerman et al., 1997; Gardner and Thompson, 1998; Ritchie, 2000; Branson, 2005) but additional studies (Chase, 1996; Oedekoven and Joern, 2000; Danner and Joern, 2003) have demonstrated that predators more effectively suppress populations under stressful abiotic conditions. Chase (1996) focused on temperature as the stressful abiotic condition and habitat choice can affect the temperature and thermoregulation of grasshoppers (Willott, 1997). Structure, specifically height and vegetation density, has a noticeable impact on microclimate (Clark, 1948; Dempster, 1955). For these reasons the structural components of habitat should be important to the survival of grasshoppers. However, few studies have examined the response of grasshoppers to habitat structure independent of plant species and most studies on the response of grasshoppers to habitat structure have not been experimental (Carpenter, 1939; Richards and Waloff, 1954; Dempster, 1955; Joern, 1982).

In this study I experimentally altered the vertical structure and density of vegetation to determine whether habitat structure is an important microhabitat characteristic for

grasshoppers independent of the composition of the plant community. I mowed alternating grid squares in a field and observed the grasshoppers within the mowed and unmowed squares. I also observed the distribution of grasshoppers along the edges of bare-ground areas created by agricultural activity. Because habitats that vary in structure also vary in predator types and density and because grasshopper species differ in their susceptibility to different predators (Belovsky et al., 1990), I expect to find species-specific preferences for habitat structure.

METHODS

Study site and species

All observations were conducted on property owned by North Carolina State University as part of the Lake Wheeler Farm Unit in Raleigh, North Carolina. Data on the usage of bare ground versus usage of vegetated ground was collected at all suitable locations on the farm unit. Data collection began on 20 July 2007 and ended on 9 October 2007.

Height of vegetation was manipulated on a single field of approximately 1,800 m² in area. This field was bordered on one side by Mid Pines Road and was otherwise surrounded by forest. Prior to the beginning of the study the field was mowed for hay, and severe drought throughout the summer restricted the growth of the vegetation.

The dominant vegetation on the field site was grass. Early in the season the grass was primarily *Fescuta*, which had been deliberately planted. Later in the season *Digitaria sanguinalis* replaced the *Fescuta* which was less drought-tolerant. *Dactylis glomerata* remained in some areas of the field throughout the study.

Helenium, *Conyza canadensis*, and *Rubus* made up most of the forbaceous cover. *Helenium* and *C. canadensis* grew more than a meter tall by the end of the season and provided

roosting perches for *Schistocerca americana*. *Rubus* was slightly more common, being more tolerant of mowing. Additionally, *Antennaria*, *Oxalis*, *Vitis rotundiflora*, and *Andropogon virginicus* were identified on the field, although none was a major component of the vegetation.

In areas where mowing was not conducted, saplings of the tree *Liquidambar styraciflua* grew up during the season. Much more rarely, saplings of *Pinus serotina* were also discovered.

This field was selected primarily because all nine species of grasshoppers included in the study were found living there, allowing identical conditions to be applied to all species. These species are: the cyrtacanthacrid, *Schistocerca americana*: two gomphocerids, *Dichromorpha viridis* and *Syrbula admirabilis*: two melanoplins, *Melanoplus femurrubrum* and *Melanoplus differentialis*; and four oedopodines, *Dissosteira carolina*, *Chortophaga viridifasciata*, *Spharagemon cristatum*, and *Hippiscus ocelote*.

Manipulation of vegetation height

Eight twenty-meter by twenty-meter squares were marked in the field. These bordered one another and formed a larger square missing one corner. The missing corner was selected to overlap with an area that had been used to park farm vehicles and was hard-packed bare earth. Alternating squares were mowed to an average height of six centimeters. These squares were classed as short plots, and were re-mowed if, at any time, any single plot was found to have an average vegetation height greater than ten centimeters during sampling. Plots were also mowed when visual assessment determined that stray forbs had grown significantly taller than the surrounding grasses. In all instances, all short plots were mowed regardless of whether

every plot satisfied the criteria for mowing. In each instance in which the short plots were mowed they were then swept for grasshoppers injured by the mower.

The remaining plots, classed as tall, were never mowed.

Observation of grasshoppers in manipulated plots

Observations of habitat usage within the manipulated habitat were restricted to a ten-meter by ten-meter square within the center of each twenty-meter by twenty-meter plot. Initial observations revealed that it was impossible for an observer to adequately focus on grasshoppers taking flight at medium range and also search the entire plot carefully for concealed grasshoppers. Therefore, each observation of a plot was conducted in two sweeps, the first focusing on grasshoppers actively escaping and the second focusing on hidden grasshoppers. Grasshoppers that were observed were identified to species in the field, and care was taken not to count the same individual grasshopper twice.

The order in which plots were swept was randomized, although an alternation between short and tall plots was always maintained. In the event of interruption by inclement weather, sampling was broken off at a point in which the number of short and tall plots sampled were the same.

Because some species of grasshoppers were capable of moving between the sampling areas of adjacent plots during their escape flights, care had to be taken in sampling adjacent plots. The direction in which the plot was swept appeared to have a high degree of influence on the direction in which escaping grasshoppers exited the plot, and the direction of sweep was chosen to drive escaping grasshoppers off the study area entirely, into a previously-sampled plot, or, when this was not possible, into whichever adjacent plot was to be sampled last.

Observation of vegetation in manipulated plots

In each instance in which observations of grasshoppers were conducted on a plot, six measurements of vegetation height were taken on the same plot within the inner sampling area. Each measurement was taken from a different location, which was selected randomly. Because selection by the investigator between adjacent plants potentially could bias the measurements the exact location was selected by an observer with his eyes closed, indicating the spot with a ruler to prevent him from feeling the height of the plants before measuring. The plant closest to the marked edge of the ruler was then measured at natural standing height. If no plant was within two centimeters of the marked edge of the ruler the area was declared bare and the height at that location was marked as zero.

At three-week intervals an additional four observations were made. The first two, cover and patchiness, characterized the extent to which the plots were covered by vegetation. Cover, estimated in five-percent increments, reflected the percentage of the plot covered by plants as viewed from above the tallest plants. Patchiness, a ranked score from one to ten, reflected the extent to which the existing bare areas were either evenly distributed or clumped together into large contiguous bare areas. This measure was independent of plant size and referred only to the uniformity of the plant distribution.

The second two observations estimated the number of forbs versus grasses on the plot. The percent of cover by forbs alone was estimated. These percentages, however, were invariably small and hard to estimate with precision. For this reason a rank for forbs was also used in which plots were assigned a score from one to five based on the forbaceous cover of the plot as compared to the other plots and surrounding areas of the field.

Investigation of habitat usage: bare ground versus cover

Throughout the period of this study, agricultural usage of the farm unit produced a number of edges between bare ground and vegetation, such as roads and the edges of tilled fields. Each edge was divided into transects based on type and height of vegetation so that each transect bordered a single type of habitat. Six equidistant measurements of vegetation height were taken along each transect. Transects were further divided into linear edges, such as dirt roads, and larger bare patches. Linear edges were always manmade, whereas bare patches were often of uncertain origin.

Edges that appeared to restrict the free movement of grasshoppers were excluded from the study.

The width of each transect was never more than two meters, one meter on each side of the edge, because grasshoppers in vegetated areas were not easily detectable beyond this limit. On occasion this sampling width was reduced if the bare area was less than one meter across. The sampling width was always equal on both sides of the edge.

I walked along each transect and recorded every grasshopper observed. Grasshoppers were identified to species in the field and their position, in bare ground or in cover, was recorded. Grasshoppers that moved forward along the transect were noted and care was taken not to count them again.

Analysis

Analysis was performed with the SAS 9.2 statistical software package. Data on vegetation height preference were analyzed with the GLMSELECT procedure which selected the general linear model with the optimal AIC from a set of model terms. Model terms included:

whether the plot was mowed or unmowed, average vegetation height on the plot, maximum vegetation measurement on the plot, the day of the study (counting up from 1), two measurements of forb cover, total vegetative cover, and the patchiness of the total vegetative cover. Population counts were reported as the percent of the daily count of any given species on a particular plot. On days when a particular species was entirely absent no percentage was recorded, resulting in the automatic exclusion of these days in the analysis for that species. This produced a dataset that was more robust against overall population trends.

A second set of general linear models was used to determine whether plot height category, average vegetation height, and maximum vegetation height were correlated. General additive models (PROC GAM) were used to determine whether the forb measurements, patchiness, or cover correlated with the plot height category, plot ID number, or time. Time was modeled nonparametrically using a smoothing parameter automatically selected using the GCV method.

Once GLMSELECT produced models, these models were run under the GLM procedure and the terms with significant p-values were graphed as regression plots using PROC REG.

For the analysis of vegetation cover GLMSELECT was used to find the general linear model with the best AIC using species, day, average vegetation height, and whether the bare area was a patch or an artificial edge. Populations were reported as the percent of any given species seen in the bare or covered area for a given transect. If a given species was absent from any given transect no percent was recorded.

GLMSELECT was also used to select models for each species. Both the all-species model and the by-species models were run in PROC GLM and Tukey tests applied to separate variables when appropriate. PROC REG was used to produce regression plots for each significant term in both the all-species and by-species models.

RESULTS

Plot characteristics

The average height for vegetation was found to be 14.7 centimeters on tall plots, and 6.6 centimeters on short plots. The average vegetation height in tall plots increased across time. No trend was detected for short plots.

Forbs were found to be more common on tall plots, a finding that was not dependent on the type of measurement used. A marginally significant result ($p = 0.0528$) was found for cover, with tall plots displaying slightly lower levels of vegetative cover than did short plots. There was no significant difference in degree of patchiness.

Habitat usage on manipulated plots

Throughout the course of the study only two grasshoppers were found with injuries consistent with those inflicted by a mower.

A total of 2,547 grasshoppers was observed on the manipulated plots. A breakdown of observations by species is provided in Table 2.1. Of special note is *Melanoplus differentialis* which was unusually uncommon in the summer of 2007 and of which only four individuals were observed.

Vegetation height

Plot class (mowed or unmowed) was significant (p value <0.5) for *Dissosteira carolina*, *Syrbula admirabilis*, *Melanoplus femurrubrum*, and *M. differentialis*. *Schistocerca americana* was correlated with average and maximum vegetation heights, but the GLMSELECT procedure found that these factors explained the presence of *S. americana* better than did models with plot height class. Both melanoplins were also correlated with average vegetation height in addition to height class of the plot. Maximum vegetation height was important for *M. femurrubrum* and was selected but not significant for *Hippiscus ocelote* and *Syrbula admirabilis*. The p-values associated with height variables are reported in Table 2.2.

All height variables were highly correlated with one another. Overall, five of the nine species of grasshopper (*Dissosteira carolina*, *Melanoplus femurrubrum*, *M. differentialis*, *Schistocerca americana*, and *Syrbula admirabilis*) showed correlations with some vegetation height variable. For all species except *D. carolina* and *Syrbula admirabilis*, grasshopper abundance increased with increasing vegetation height. Figure 2.1 shows the relative abundance of the five species with vegetation height preferences in mowed versus unmowed plots. R-squared values for quantitative comparisons are reported in Table 2.3.

Forbs

Five species showed significant correlations with the rank or percent measures of forbs in a given plot. These species were *Dichromorpha viridis*, *Melanoplus femurrubrum*, *Hippiscus ocelote*, *Schistocerca americana*, and *Spharagemon cristatum*. P-values for these comparisons are shown in Table 2.4. Of these species only *D. viridis* showed a decrease in abundance as the percent of forbs on a plot increased.

Patchiness

Habitat patchiness showed significant correlations with abundance in five species: *Chortophaga viridifasciata*, *Dichromorpha viridis*, *Dissosteira carolina*, *Melanoplus femurrubrum*, and *Schistocerca americana*. P-values for these comparisons are shown in Table 2.5. *Dissosteira carolina* and *Schistocerca americana* increased in abundance as the habitat became patchier while the other three species decreased in abundance. All R-squared values were quite low, however, with none of them greater than 0.1.

Habitat usage: bare ground versus cover

A total of 2,274 grasshoppers was observed on the edge transects. The breakdown of observations by species can be found in Table 2.6.

Species

Species was a significant factor (p-value <0.0001) in the model comparing all species to each other. Two major groups came out of the Tukey tests: *Dissosteira carolina* and *Spharagemon cristatum* were statistically indistinguishable from one another and showed a strong preference for bare ground. *Dichromorpha viridis*, *Melanoplus femurrubrum*, *M. differentialis*, *Schistocerca americana*, and *Syrbula admirabilis* formed another group which showed a strong preference for vegetative cover. *Chortophaga viridifasciata* and *Hippiscus ocelote* were indistinguishable from one another but not consistently distinguishable from members of the group preferring vegetative cover. A complete table of comparisons is shown in Table 2.7 and a chart of microhabitat usage can be found in Figure 2.2.

Other factors

Very few other factors showed significant correlation with the abundance of grasshoppers on the transects. *Hippiscus* showed a significant correlation (p-value <0.0001) with time, with *Hippiscus* more likely to be in cover later in the season. It is possible that this is a sampling artifact as *Hippiscus* became available on many more plots later in the season.

Chortophaga viridifasciata was more likely to be found on bare ground in areas where the average vegetation height was higher (p-value 0.0052, R-squared 2196).

DISCUSSION

Overall the habitat preferences found for the species under study closely resemble those found in previous studies with only oedopodines preferring bare ground in the transect studies and vegetation height preferences varying by species in the vegetative height studies.

Both gomphocerids were found to prefer cover as expected from Capinera and Sechrist (1982) who found gomphocerids associated with high-biomass grassland.

Dichromorpha viridis followed general patterns established for this species. A number of studies have established that this is a species associated with thick vegetation or wetter habitat, either quantitatively or in habitat notes (Rehn and Hebard, 1910, 1916; Hebard, 1925; Isely, 1937; Friauf, 1953; Squitier and Capinera, 2002). Craig et al. (1999) had found the gomphocerids to be more common in grassy habitats and *D. viridis* also followed this trend, being negatively associated with forbs. Despite a strong preference for vegetative cover *D. viridis* did not show a preference for vegetation height. This supports comments made by Isely (1946) in which he notes that *D. viridis* lives under grass shoots and can be found even in very short grass. Otte (1981) similarly noted that *D. viridis* is often associated with short grass. *D. viridis* demonstrates clearly the value of separating vegetative height from vegetative density.

Isely (1938 and 1946) commented that the other gomphocerid studied here, *Syrbula admirabilis*, preferred taller, mature grass. This was not born out in the present study in which *Syrbula* showed a preference for shorter grass. Some of this may be geographic variation. Isely's study was conducted in Texas while Rehn and Hebard's 1916 survey in the southeastern United States, including North Carolina, found *Syrbula admirabilis* in overgrown fields and short grass while Cross et al. (1997) recorded it in oldfields in South Carolina. While this species seems to have a broader range of habitats than some others the present study did bear out previous associations with thick grass or undergrowth rather than bare ground (Isely, 1937; Whelan, 1938; Friauf, 1953; Squitier and Capinera, 2002).

Melanoplines have previously been considered inhabitants of thicker and often forbaceous growth (Capinera and Sechrist, 1982; Craig et al., 1999), a conclusion the present study also supported.

Reports by Hebard (1931), Dowdy (1950), and Cross et al. (1997) support forbivory in *M. femurrubrum*, consistent with the increase in this species' density in plots with forbs. Cropland is a frequently described habitat for this species (Rehn and Hebard, 1909; Hebard, 1925) as are wetter areas in drier states (La Rivers, 1948; Rehn and Hebard, 1909). While this would tend to suggest a species that prefers high, dense growth, the magnitude of this preference was not extreme. Bare ground in the transect study was avoided more assiduously than was short grass in the vegetation-height manipulation study with 27.4% of individuals found in mowed plots. This preference may also be expected to be linked to the presence of additional forbs on unmowed plots.

Melanoplus differentialis, by contrast, had distinct preferences for both cover and tall grass despite low sample sizes. Previous records concerning this species are almost all from human-disturbed habitat. Rehn and Hebard (1909) collected their specimens from croplands and tall weeds. Hebard (1925) later recorded the habitat of this species as croplands and “rank patches of weeds on disturbed ground”. Isely (1946) similarly recorded this species in tall non-native vegetation. While Whelan (1938) found *M. differentialis* in low prairie in Nebraska, records of this species in native vegetation are oddly uncommon.

The single cyrticanthacridid in this study, *Schistocerca americana*, has previously been reported as something of a habitat generalist (Blatchley, 1920). Squitier and Capinera (2002) found *Schistocerca americana* in more of their study habitats than any other species. Other work has found them in agricultural fields (Tinkham, 1948), open forest (Friauf, 1953; Capinera et al., 1997), and oldfields (Cross et al., 1997). Agricultural habitats and oldfields dominated in Squitier’s and Capinera’s (2002) study as well. Given this, it was not surprising to find *Schistocerca americana* strongly linked both to cover and vegetation height. Vegetation height seems particularly important for this species. In analysis both average and maximum vegetation height were positively linked to the abundance of this species but height class was not. The simplest explanation is that not all unmowed plots reached the same average grass height and that *Schistocerca* was preferentially attracted to very tall vegetation. The importance of maximum vegetation height along with personal observation of roosting *Schistocerca* suggests that this species prefers at least occasional vegetation of extreme height.

The oedopodines proved less consistent in habitat preference than were the other subfamilies. Craig et al. (1999), Capinera and Sechrist (1982), and Blatchley (1920) noted that

this group tends to be present in more sparsely-vegetated habitats. Sparsely vegetated habitats are often populated by height-restricted plants and so the ability to separate preference for bare ground from preference for short vegetation was of special importance for the four members of this group.

Two species, *Dissosteira carolina* and *Spharagemon cristatum*, behaved as expected. *D. carolina* is well-known from roads both to the casual observer and in the scientific literature (Rehn and Hebard, 1916; Hebard, 1925; Whelan, 1938) and is often associated with disturbed or sparse habitat (Rehn and Hebard, 1909; Blatchley, 1920; Friauf, 1953; Craig et al., 1999). *D. carolina* showed a strong preference for bare ground in the transects in this study. However, despite this preference it showed only a weak preference for short versus tall vegetation. This may make sense of out Isely's (1937) record of *D. carolina* as an occasional species in deep soil (well-vegetated) habitat.

Spharagemon cristatum is normally picked up in samples on sandy soils (Isely, 1937; Tinkham, 1948) although records exist of it from cropland (Squitier and Capinera, 2002). (Rehn and Hebard [1916] contains references to *S. collare* on sandy soil in North Carolina. At this time *S. cristatum* was considered a subspecies of *S. collare*, making it likely that these records refer to *S. cristatum*.) Squitier and Capinera also recorded *S. cristatum* in pine plantations where it was strongly linked to open canopy. Again, this suggests a microhabitat preference born out in the present study in which *S. cristatum* preferred bare ground but showed no preference for vegetation height.

The remaining two oedopodines showed much less "typical" behavior. Neither showed a preference for bare ground or short grass. This may be related to phylogeny, as

Dissosteira carolina and *Spharagemon cristatum* are closely related, while *Chortophaga viridifasciata* appears to be a basal oedopodine (Chapco, 1997). Several existing records from the American West present data to suggest that *C. viridifasciata* is a tall-grass species (Hebard, 1925; Isely, 1937, 1938; Carpenter, 1939; Craig et al., 1999). Otte (1984) and Rehn and Hebard (1916) both refer to *C. viridifasciata* as an inhabitant of shorter grass. Given more recent suggestions that *C. australior* may represent a habitat-associated phenotype of *C. viridifasciata* and not a separate species (Brust et al., 2008) it is worth noting two records of *C. australior* in Florida, where it appeared more closely associated with bare areas. Friauf (1953) found *C. australior* to be associated with sandy habitat while Squitier and Capinera (2002) frequently found it along roadsides. In this study *Chortophaga viridifasciata* appeared to be a species of intermediate habitat in regards to both vegetation height and cover.

Hippiscus is a species for which overall data are rather poor. Following Otte (1984), *H. rugosus* is treated as a synonym for *H. ocelote*. *H. rugosus* has been recorded from thicker vegetation (Isely, 1937), poorer vegetation (Hebard, 1925), dry uplands (Blatchley, 1920), fields (Rehn and Hebard, 1910) and forest (Rehn and Hebard, 1910, 1916; Tinkham, 1948). In the present study *Hippiscus* showed no extreme preferences. Its preference for forbs was unique amongst the oedopodines and bears further investigation.

This study demonstrates that grasshoppers can disassociate vegetative cover from vegetative height when choosing habitat and that selection can be based on either one or both of these variables. This selection can occur independently of selection for plant or soil type. However, this does not negate the value of plant species and soil type for habitat selection. Neither plant species nor soil type were the focus of this study but both are expected to act by

limiting the habitat available to grasshoppers. Habitats without the correct plant species or soil suitable for oviposition should not be expected to support populations of grasshoppers.

Similarly, habitats without the correct vegetation structure may not support grasshoppers despite the presence of food and soil suitable for oviposition.

The mechanism by which vegetation structure makes habitat suitable or unsuitable remains to be investigated. *Chortophaga* shows some tendency to expand its use of bare ground in areas where the vegetation is tall which is consistent with the hypothesis that vegetation structure acts on grasshoppers by altering the microclimate. However, if microclimate is an important factor in regulating habitat usage by grasshoppers habitat-switching in other climates might be expected. This phenomenon could explain the sometimes-contradictory qualitative reports of grasshopper's habitat preferences from different states, but quantitative data are lacking. Similarly, habitat-switching under differing predation conditions might also be expected if vegetation structure is primarily used as cover from predators. Again, quantitative habitat data under differing conditions are not present.

LITERATURE CITED

- Agrawal, A. A., & Karban, R. (1997). Domatia mediate plant-arthropod mutualism. *Nature*, 387, 562-563.
- Anderson, N. L. (1964). Some relationships between grasshoppers and vegetation. *Annals of the Entomological Society of America*, 57, 736-742.
- Anderson, R. V., Tracy, C. R., & Abramsky, Z. (1979). Habitat selection in two species of short-horned grasshoppers. The role of thermal and hydric stresses. *Oecologia*, 38(3), 359-374.
- Babbitt, K. J., & Tanner, G. W. (1998). Effects of cover and predator size on survival and development of *Rana utricularia* tadpoles. *Oecologia*, 114(2), 258-262.

- Beckerman, A. P., Uriarte, M., & Schmitz, O. J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences of the United States of America*, 94(20), 10735-10738.
- Belovsky, G. E., & Slade, J. B. (1993). The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos*, 68(2), 193-201.
- Belovsky, G. E., Slade, Jennifer B., & Stockhoff, B. A. (1990). Susceptibility to predation for different grasshoppers: An experimental study. *Ecology*, 71(2), 624-634.
- Blatchley, W. S. (1920). *Orthoptera of northeastern America*. Indianapolis: The Nature Publishing Company.
- Bock, C. E., Bock, J. H., & Grant, M. C. (1992). Effects of bird predation on grasshopper densities in an Arizona grassland. *Ecology*, 73(5), 1706-1717.
- Branson, D. H. (2005). Direct and indirect effects of avian predation on grasshopper communities in northern mixed-grass prairie. *Environmental Entomology*, 34(5), 1114-1121.
- Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? *Oecologia*, 135, 407-413.
- Brust, M. L., Hoback, W. W., & Wright, R. J. (2008). A Review of the genus *Chortophaga* (Orthoptera: Acrididae) among Nebraska populations: Questioning the validity of *Chortophaga australior* Rehn and Hebard. *Journal of Orthoptera Research*, 17(1), 101-105.
- Capinera, J. L., & Sechrist, T. S. (1982). Grasshopper (Acrididae)--host plant associations: Response of grasshopper populations to cattle grazing intensity. *Canadian Entomologist*, 114(11), 1055-1062.
- Capinera, J. L., Scherer, C. W., & Simkins, J. B. (1997). Habitat associations of grasshoppers at the MacArthur Agro-Ecology Research Center, Lake Placid, Florida. *The Florida Entomologist*, 80(2), 253-261.
- Carpenter, J. R. (1939). Fluctuations in biotic communities, V. Aspection in a mixed-grass prairie in Central Oklahoma. *American Midland Naturalist*, 22(2), 420-435.
- Cepek, J. D. (2004). Diet composition of coyotes in the Cuyahoga Valley National Park, Ohio. *Ohio Journal of Science*, 104(3), 60-64.

- Chapco, W., Martel, R., & Kuperus, W. (1997). Molecular phylogeny of North American band-winged grasshoppers (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 90(5), 555-562.
- Chase, J. M. (1996). Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos*, 77, 495-506.
- Clark, E. J. (1948). Studies in the ecology of British grasshoppers. *Transactions of the Royal Entomological Society of London*, 99, 173-222.
- Clark, T. L., & Messina, F. J. (1998). foraging behavior of lacewing larvae (Neuroptera: Chrysopidae) on plants with divergent architectures. *Journal of Insect Behavior*, 11(3), 303-317.
- Clark, T. L., & Messina, F. J. (1998). Plant architecture and the foraging success of ladybird beetles attacking the Russian wheat aphid. *Entomologia Experimentalis et Applicata*, 86(2), 153-161.
- Craig, D. P., Bock, Carl E, Bennett, B. C., & Bock, Jane H. (1999). habitat relationships among grasshoppers (Orthoptera: Acrididae) at the western limit of the great plains in Colorado. *American Midland Naturalist*, 142(2), 314-327.
- Cross, W. H., Cross, W. M., Jackson, P. R., Dixon, P. M., & Pinder, J. E. (1997). Corresponding development of plant and phytophagous orthopteran communities during southeastern old-field Succession. *American Midland Naturalist*, 137(1), 188-193.
- Crowder, L. B., & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology*, 63(6), 1802-1813.
- Danner, B. J., & Joern, Anthony. (2003). Resource-mediated impact of spider predation risk on performance in the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). *Oecologia*, 137(3), 352-359.
- Dempster, J. P. (1955). Factors affecting small scale movements of some British grasshoppers. *Proceedings of the Royal Entomological Society of London*, 30, 145-150.
- Dowdy, W. W. (1950). A community study of an oak-hickory association with special reference to invertebrates. *American Midland Naturalist*, 43(3), 667-695.
- Finke, D. L., & Denno, R. F. (2002). Intraguild predation diminished in complex-structured vegetation: Implications for prey suppression. *Ecology*, 83(3), 643-652.
- Fowler, A. C., Knight, R. L., George, T. L., & McEwen, L. C. (1991). Effects of avian predation on grasshopper populations in North Dakota grasslands. *Ecology*, 72(5), 1775-1781.

- Friauf, J. J. (1953). An ecological study of the Dermaptera and Orthoptera of the Welaka Area in northern Florida. *Ecological Monographs*, 23(2), 79-126.
- Gardner, K. T., & Thompson, D. C. (1998). Influence of avian predation on a grasshopper (Orthoptera: Acrididae) assemblage that feeds on threadleaf snakeweed. *Environmental Entomology*, 27(1), 110-116.
- Geitzenauer, H. L., & Bernays, E. A. (1996). Plant effects on prey choice by a vespid wasp, *Polistes arizonensis*. *Ecological Entomology*, 21, 227-234.
- Gillett, S. D., & Gonta, E. (1978). Locust as prey: Factors affecting their vulnerability to predation. *Animal Behaviour*, 26(1), 282-289.
- Glass, N. R. (1971). Computer analysis of predation energetics in the largemouth bass. In B. C. Patten (Ed.), *Systems analysis and simulation in ecology* (Vol. 1, pp. 325-363). New York, New York: Academic Press.
- Grevstad, F. S., & Klepetka, B. W. (1992). The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia*, 92(3), 399-404.
- Groner, E., & Ayal, Y. (2001). The interaction between bird predation and plant cover in determining habitat occupancy of darkling beetles. *Oikos*, 93(1), 22-31.
- Gunnarsson, B. (1990). Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology*, 59(2), 743-752.
- Hanks, L. M., & Denno, R. F. (1993). Natural enemies and plant water relations influence the distribution of an armored scale insect. *Ecology*, 74(4), 1081-1091.
- Hebard, M. (1925). The Orthoptera of South Dakota. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 77, 33-155.
- Hebard, M. (1931). The Orthoptera of Kansas. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 83, 119-227.
- Hurd, L. E., & Eisenberg, R. M. (1990). Arthropod community responses to manipulation of a birophic predator guild. *Ecology*, 71, 2107-2114.
- Isely, F. B. (1937). Seasonal succession, soil relations, numbers, and regional distribution of North-Eastern Texas acridians. *Ecological Monographs*, 7(3), 317-344.
- Isely, F. B. (1938). The relations of Texas acrididae to plants and soils. *Ecological Monographs*, 8(4), 551-604.

- Isely, F. B. (1946). Differential feeding in relation to local distribution of grasshoppers. *Ecology*, 27(2), 128-138.
- Joern, Anthony. (1982). Vegetation structure and microhabitat selection in grasshoppers (Orthoptera, Acrididae). *Southwestern Naturalist*, 27(2), 197-209.
- Joern, Anthony. (1986). Experimental study of avian predation on coexisting grasshopper populations (Orthoptera: Acrididae) in a sandhills grassland. *Oikos*, 46, 243-249.
- Joern, Anthony. (1992). Variable impact of avian predation on grasshopper assemblies in sandhills grassland. *Oikos*, 64(3), 458-463.
- Joern, Anthony, & Lawlor, L. R. (1980). Food and microhabitat utilization by grasshoppers from arid grasslands: Comparisons with neutral models. *Ecology*, 61(3), 591-599.
- Joern, Anthony, & Lawlor, L. R. (1981). Guild structure in grasshopper assemblages based on food and microhabitat resources. *Oikos*, 37, 93-104.
- Joern, Anthony, & Rudd, N. T. (1982). Impact of predation by the robber fly *Proctacanthus milbertii* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. *Oecologia*, 55(1), 42-46.
- Judd, S. D. (1899). The efficiency of some protective adaptations in securing insects from birds. *The American Naturalist*, 33(390), 461-484.
- Kaiser, H. (1983). Small scale spatial heterogeneity influences predation success in an unexpected way: Model experiments on the functional response of predatory mites (Acarina). *Oecologia*, 56(2/3), 249-256.
- La Rivers, I. (1948). A synopsis of Nevada Orthoptera. *American Midland Naturalist*, 39(3), 652-720.
- Landry, S. O. J. (1970). The Rodentia as omnivores. *The Quarterly Review of Biology*, 45(4), 351-372.
- Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, 139(1), 1-10.
- Leber, K. M. (1985). The influence of predatory decapods, refuge, and microhabitat selection on seagrass communities. *Ecology*, 66, 1951-1964.
- Lewis, D. B., & Eby, L. A. (2002). Spatially heterogeneous refugia and predation risk in intertidal salt marshes. *Oikos*, 96(1), 119-129.

- Messina, F. J., Jones, T. A., & Nielson, D. C. (1997). Host-plant effects on the efficacy of two predators attacking Russian wheat aphids (Homoptera: Aphididae). *Environmental Entomology*, 26(6), 1398-1404(7).
- Moore, J. E., & Strickland, E. H. (1954). Notes on the food of three species of Alberta amphibians. *American Midland Naturalist*, 52(1), 221-224.
- Oedekoven, M. A., & Joern, A. (2000). Plant quality and spider predation affects grasshoppers (Acrididae): Food-quality dependent compensatory mortality. *Ecology*, 81(1), 66-77.
- Otte, D. (1981). *The North American grasshoppers: Volume I*. Cambridge, MA: Harvard University Press.
- Otte, D. (1984). *The North American grasshoppers: Volume II*. Cambridge, MA: Harvard University Press.
- Plummer, M. V. (1981). Habitat utilization, diet and movements of a temperate arboreal snake (*Opheodrys aestivus*). *Journal of Herpetology*, 15(4), 425-432.
- Rehn, J. A. G., & Hebard, M. (1909). An orthopterological reconnaissance of the southwestern United States. Part II: New Mexico and Western Texas. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 61(1), 111-175.
- Rehn, J. A. G., & Hebard, M. (1910). Preliminary studies of North Carolina Orthoptera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 62(3), 615-650.
- Rehn, J. A. G., & Hebard, M. (1916). Studies of the Dermaptera and Orthoptera of the coastal plain and Piedmont region of the southeastern United States. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 68, 87-1314.
- Richards, O. W., & Waloff, Z. (1954). Studies on the biology and population dynamics of British grasshoppers. *Anti-Locust Bulletin*, 17, 182 pp.
- Ritchie, M. E. (2000). Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology*, 81, 1601-1612.
- Rypstra, A. L., Carter, P. E., Balfour, R. A., & Marshall, S. D. (1999). Architectural features of agricultural habitats and their impact on the spider inhabitants. *Journal of Arachnology*, 27(1), 371-377.
- Schmitz, O. J., & Suttle, K. B. (2001). Effects of top predator species on direct and indirect interactions in a food web. *Ecology*, 82(7), 2072-2081.

- Squitier, J. M., & Capinera, J. L. (2002). Habitat associations of Florida grasshoppers (Orthoptera: Acrididae). *The Florida Entomologist*, 85(1), 235-244.
- Stidham, J. A., & Stidham, T. A. (2008). Bull nettle (*Cnidoscolus texanus*) as enemy free space for Orthopterans in Texas, U.S.A. *Entomological News*, 119(1), 102-104.
- Sunderland, K., & Samu, F. (2000). Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata*, 95(1), 1-13.
- Tinkham, E. R. (1948). Faunistic and ecological studies on the Orthoptera of the Big Bend region of Trans-Pecos Texas, with especial reference to the orthopteran zones and faunae of Midwestern North America. *American Midland Naturalist*, 40(3), 521-663.
- Whelan, D. B. (1938). Orthoptera of an Eastern Nebraska prairie. *Journal of the Kansas Entomological Society*, 11(1), 3-6.
- Willott, S. J. (1997). Thermoregulation in four species of British grasshoppers (Orthoptera: Acrididae). *Functional Ecology*, 11(6), 705-713.
- Yang, L. H. (2000). Effects of body size and plant structure on the movement ability of a predaceous stinkbug, *Podisus maculiventris* (Heteroptera: Pentatomidae). *Oecologia*, 125(1), 85-90.

Table 2.1. Numbers of each species of grasshopper observed on manipulated plots. Numbers reported are observations, not individuals.

Species	Number of Observations
<i>Chortophaga viridifasciata</i>	514
<i>Hippiscus ocelote</i>	21
<i>Spharagemon cristatum</i>	250
<i>Dissosteira carolina</i>	207
<i>Melanoplus differentialis</i>	4
<i>Melanoplus femurrubrum</i>	1261
<i>Schistocerca americana</i>	80
<i>Dichromorpha viridis</i>	173
<i>Syrbula admirabilis</i>	37

Table 2.2. P-values for vegetation height variables as predictors of grasshopper abundance on plots. Height class denotes mowed or unmowed plots, while the other measures are drawn from direct vegetation measurements. Only significant p-values (<0.5) that were selected by the model selection procedure are reported.

Species	Height Class	Average Height	Maximum Height
<i>Melanoplus differentialis</i>	0.0024	0.0494	
<i>Dissosteira carolina</i>	<.0001		
<i>Melanoplus femurrubrum</i>	0.0028	0.0002	0.0133
<i>Schistocerca americana</i>		<.0001	0.0045
<i>Syrbula admirabilis</i>	0.0139		

Table 2.3. R-squared values for correlations between grasshopper abundance on a given plot and vegetation height measurements. Only significant (p-value <0.5) comparisons are reported.

Species	Average height	Maximum height
<i>Melanoplus differentialis</i>	0.0059	
<i>Melanoplus femurrubrum</i>	0.2458	0.1372
<i>Schistocerca americana</i>	0.1971	0.0842

Table 2.4. P-values for significant correlations between per-plot abundance of grasshoppers and the two measures of forb cover. Only significant values (<0.5) are reported. *Dichromorpha viridis* was the only species for which this correlation had a negative slope.

	Forbs rank	Forbs percent
<i>Dichromorpha viridis</i>	0.065	0.0039
<i>Dissosteira carolina</i>		
<i>Hippiscus ocelote</i>	<.0001	<.0001
<i>Melanoplus femurrubrum</i>	0.0046	
<i>Schistocerca americana</i>	0.0002	
<i>Spharagemon cristatum</i>	0.0272	

Table 2.5. P-values for significant correlations between per-plot abundance of grasshoppers and the patchiness of habitats. Only *Dissosteira carolina* and *Schistocerca americana* preferred patchier habitat. Only significant values (<0.5) are reported.

<i>Chortophaga viridifasciata</i>	0.031
<i>Dichromorpha viridis</i>	<.0001
<i>Dissosteira carolina</i>	0.003
<i>Melanoplus femurrubrum</i>	<.0001
<i>Schistocerca americana</i>	0.0246

Table 2.6. Numbers of each species of grasshopper observed along edge transects. Numbers reported are observations, not individuals.

Species	Number of Observations
<i>Chortophaga viridifasciata</i>	114
<i>Hippiscus ocelote</i>	84
<i>Spharagemon cristatum</i>	114
<i>Dissosteira carolina</i>	724
<i>Melanoplus differentialis</i>	57
<i>Melanoplus femurrubrum</i>	809
<i>Schistocerca americana</i>	224
<i>Dichromorpha viridis</i>	121
<i>Syrbula admirabilis</i>	27

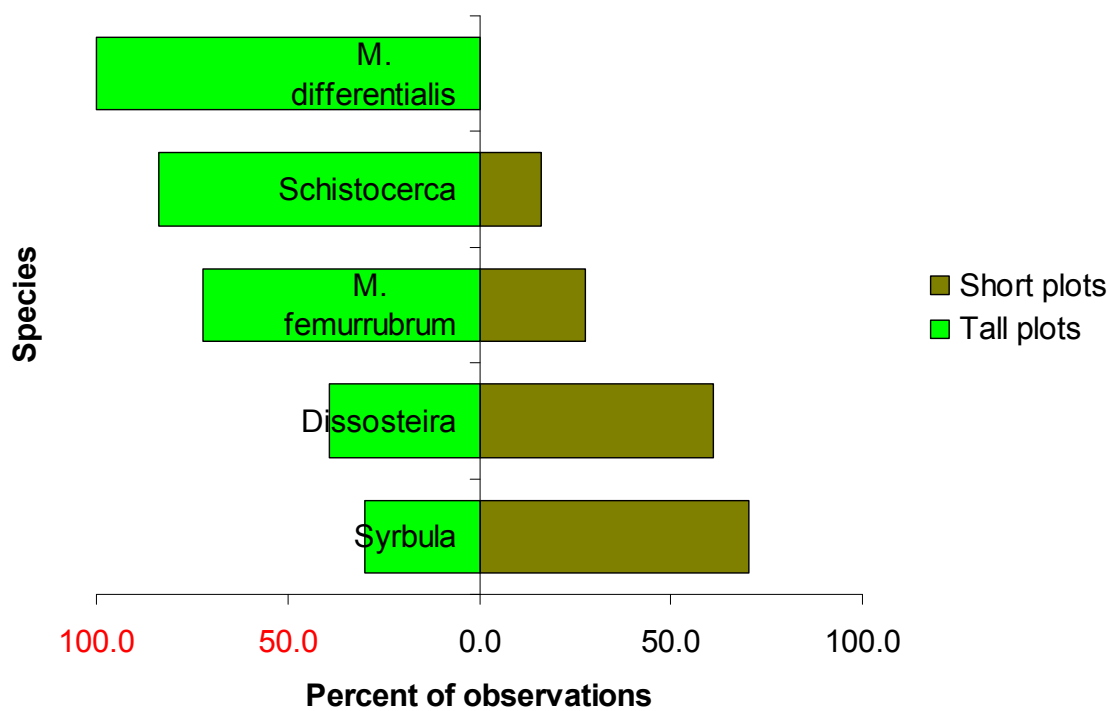


Figure 2.1.

The percent of observations made in short and tall plots by species. Only species for which a vegetation height variable was statistically significant at an alpha level of 0.05 are included.

Species are ordered from top to bottom by their usage of tall grass plots.

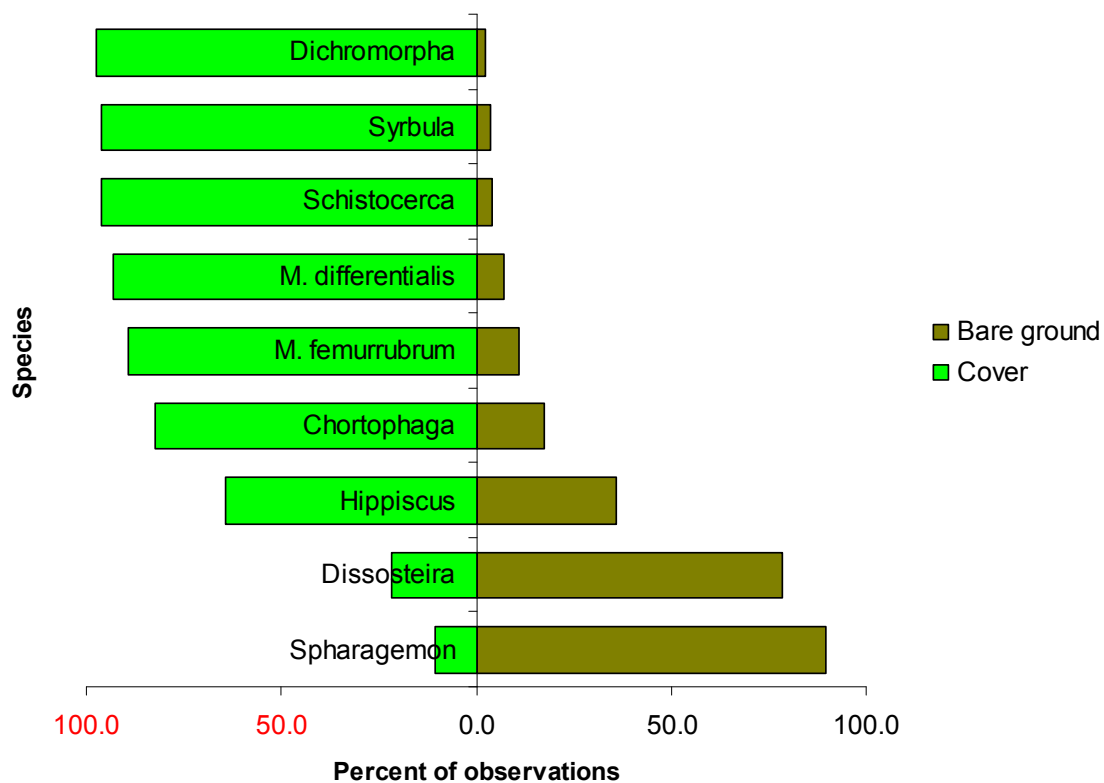


Figure 2.2.

The percent of observations made on the bare side and covered side of the edge transects by species. Species are ordered from top to bottom in decreasing usage of grass cover.

CHAPTER THREE

SPECIES-SPECIFIC ESCAPE BEHAVIOR IN GRASSHOPPERS

INTRODUCTION

All prey animals are forced to balance the demands of foraging with the demands of escaping predation. On short time scales these demands take the form of a decision by the animal to flee from the patch on which it is foraging. This decision is expected to occur when a prey animal perceives a level of threat from the predator sufficient to negate the benefits of continued foraging (Ydenberg and Dill, 1986). This decision is expected to be further modified by camouflaged prey, in which the decision to flee also negates the protective value of camouflage (Broom and Ruxton, 2005) and can cause individuals that are cryptic to tolerate closer approaches by predators than do less-cryptic individuals (Heatwole, 1968; Martin et al., 2009; Cuadrado et al., 2001; Cooper et al., 2008; Cabido et al., 2009). The distance at which a prey animal can be detected may also be relevant for explaining sized-based differences in reactions to predators that have been found in some studies (Smith, 1997; Cuadrado et al., 2001; Blumstein et al., 2005; Dangles et al., 2007).

Because the threat of predation is dependent upon the ability of the prey species to escape we should expect to see interspecific differences in the distance at which flight is initiated (hereafter flight-initiation distance, abbreviated to FID) and the distance flown by prey animals (hereafter abbreviated to flight distance or FD) faced with the same predatory threat, something that has been experimentally verified in several vertebrate taxa (Heatwole, 1968; Fernandez-Juricic et al., 2002; Blumstein, 2003a; Blumstein et al., 2005). Fewer data exist for invertebrates but studies on fiddler crabs (Frix et al., 1991) have shown species-dependent differences in the distance crabs flee down their burrows after an attack.

Cooper (2006) examined a single species of grasshopper and determined that the responses of this grasshopper to a model predator were consistent with the theories derived from observations on vertebrates. Joern (1988) observed differences in the distances from which grasshopper sparrows would attack different species of grasshoppers which suggests that species-specific FIDs are present in grasshoppers. However, to the best of my knowledge this has not been explicitly tested for grasshoppers or for any other invertebrate species.

I examined escape behavior in nine species of grasshoppers in an environment where they occur naturally. The FID, FD, and angle of escape was examined in regard to the species of grasshopper and numerous environmental characteristics that may have influenced the escape decision. If grasshoppers make escape decisions in a similar manner to vertebrates, FIDs and possibly FDs should vary with species. Larger grasshoppers are also expected to have longer FIDs and FDs.

METHODS

Study site and species

This study was conducted on the Lake Wheeler Farm Unit in Raleigh, North Carolina. Field research was carried out between 7 September 2007 and 6 August 2010 during the warm-weather period extending from June to mid-October.

Sites within the farm unit were chosen on the basis of the species of grasshoppers present, whether the site manager would grant permission, and the presence of a suitably large unobstructed open area in which to pursue grasshoppers. Within the available sites that fulfilled those criteria the vegetation varied greatly in species and in height. Because many

variables can influence the cost of leaving a patch of ground it was thought best to utilize all available sites with the target species of grasshoppers.

Nine species of orthopterans were included in this study: two gomphocerids (*Dichromorpha viridis* and *Syrbula admirabilis*) a cyrtacanthacridid (*Schistocerca americana*) two melanoplins (*Melanoplus femurrubrum* and *M. differentialis*) and four oedopodines (*Chortophaga viridifasciata*, *Hippiscus ocelote*, *Spharagemon cristatum*, and *Dissosteira carolina*).

Observation of escape behavior

All observations of escape behavior were carried out by two observers, one in the role of a flusher and one in the role of a marker. The flusher was always dressed in the same clothes to avoid evoking different responses by the grasshoppers due to changes in the flusher's appearance (Gutzwiller and Marcum, 1997). The flusher preceded the marker through the field and located grasshoppers. Once located, the grasshopper's external temperature was measured with a Sixth Sense LT100 infrared surface temperature meter held fifteen centimeters or closer to the grasshopper. The observers then moved away from the animal to allow it to return to a lower state of alertness. Once the grasshopper had adopted a resting posture again the flusher walked towards the grasshopper at a practiced constant pace of 1.59 m/s, until the grasshopper initiated escape behavior (flushed). The use of a human as a model predator is consistent with prior studies on species which are not locally preyed upon by humans (Amo et al., 2007; Blumstein, 2003a; Blumstein et al., 2005; Cooper et al., 2008; Cuadrado et al., 2001; Fernandez-Juricic et al., 2002; Goodman, 2009; Gutzwiller and Marcum, 1997; Heatwole, 1968). If the grasshopper did not move the flusher would touch

the grasshopper with his foot (or hand in the case of grasshoppers perched on tall vegetation). Once the grasshopper moved, or, failing to move, was touched without an escape response, the flusher placed markers at the location of both himself and the grasshopper when the grasshopper flushed. The marker tracked the grasshopper during its escape attempt and marked the point at which it settled and stopped moving.

The three locations were designated as flusher position (location of the flusher when the animal flushed), flush position (the location from which the animal flushed), and landing position (the location at which the flushed animal landed). Ground temperature was measured at the flush position, again with the Sixth Sense LT100 infrared surface temperature meter. At both flush and landing positions the height of the vegetation was measured at the exact position and at five evenly-spaced points two centimeters from the exact location. Measurements were rounded to the nearest centimeter. If no vegetation existed at a point a height of zero was recorded. The distance between flusher position and flush position (FID) was measured with a Stanley FaxMax laser measuring tape, as was the distance between the flush and landing positions (flight distance). The straight line connecting the flusher and flush positions was designated as the approach line and the straight line connecting the flush and landing positions was dubbed the escape path. The smaller of the angles between the approach path and the escape path was measured to the nearest ten degrees.

During the 2010 field season a third person with a new role was added to the team. This person captured the grasshopper once it completed its flight. The captured grasshopper was individually bagged along with two unique identification tags and frozen.

Handling of specimens

Fifty specimens of each species studied were taken from the NCSU Entomology Department collection. These were measured, from the front of the head to the tip of the forewings or abdomen, whichever extended furthest back.

Specimens collected in the 2010 field season were sexed, and sorted by color pattern. Two lengths were measured on each animal: (1) from the front of the head to the end of the forewings and (2) from the front of the head to the tip of the abdomen. Animals were thawed and straightened for measuring.

All the specimens were dried at room temperature in a sealed container containing Drierite. Specimens were left in open bags to keep all body parts and tags with the specimen. Drierite was changed when the indicating Drierite changed color. Dry specimens were weighed to the nearest fiftieth of a gram, a level of precision that revealed individual variation.

Identification of predators

Throughout the course of the study potential avian predators of grasshoppers were observed in order to determine the threats they posed for grasshoppers on the study site. Notable species included the American kestrel (*Falco sparverius*), the eastern meadowlark (*Sturnella magna*), European starling (*Sturnus vulgaris*), killdeer (*Charadrius vociferus*), the northern cardinals (*Cardinalis cardinalis*), and the eastern bluebird (*Sialia sialis*). Previous studies have shown that American kestrels, eastern meadowlarks, killdeer, and eastern bluebirds feed on grasshoppers (Anderson et al., 1993; Balgooyen, 1997; Pinkowski, 1978; Kennedy, 1950; Lindsey, 1939). Personal observations confirmed that both bluebirds and

cardinals feed on grasshoppers. Additional species sighted on the field site that might opportunistically take grasshoppers included the fish crow (*Corvus ossifragus*), Carolina chickadee (*Poecile carolinensis*), red-tailed hawk (*Buteo jamaicensis*), brown-headed cowbird (*Molothrus ater*), eastern phoebe (*Sayornis phoebe*), song sparrow (*Melospiza melodia*), rufous-sided towhee (*Pipilo erythrophthalmus*), chipping sparrow (*Spizella passerine*), northern flicker (*Colaptes auratus*), savannah sparrow (*Passerculus sandwichensis*), American robin (*Turdus migratorius*), blue jay (*Cyanocitta cristata*), blue grosbeak (*Passerina caerulea*), and red-winged blackbird (*Agelaius phoeniceus*). Of these species, starlings, red-tailed hawks, cowbirds, all three species of sparrow, towhees, robins, and blue grosbeaks were observed feeding on the ground in areas inhabited by grasshoppers.

Two attempts were made to identify potential small mammalian predators. For five days beginning on 29 September 2009 and for four days starting on 21 January 2010 Sherman traps were set in fields used in the study. During the first period 20 traps were set, and during the second period 50 traps were set. Traps were baited with a mixture of peanut butter, oats, and bacon bits. On both occasions *Peromyscus leucopus* was the only animal caught.

Larger mammalian predators were identified during a week-long period beginning on 29 September 2009. A motion-activated camera was set in the wooded border between two fields and tuna, corn, and beef were placed in front of the camera. Three potentially insectivorous species were identified from the photographs taken by the camera: raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and gray fox (*Urocyon cinereoargenteus*). All three species are known to eat grasshoppers (Nicholson, 1985; Hockman and Chapman,

1983; Hamilton, 1951), and raccoons are known to successfully prey upon even the fast-flying *Dissosteira carolina* (Giles, 1940).

Anoles (*Anolis carolinensis*) and toads (*Bufo woodhousii*) were sighted within the study area on several occasions.

Temperature data

Local temperature data were obtained from NOAA for each sampling day. The dataset used was from the weather station Raleigh 4 SW, the closest station to the field site.

Statistical Analysis

All statistical analyses were performed with the SAS 9.2 software package.

Initially the GLM procedure was used to determine if there was any effect of species on FID or flight distance in the unmanipulated data without other model terms.

Selection of a more complex model was carried out using the GLMSELECT procedure using AIC as the selection criterion and using a stepwise selection process. Models were selected for three variables of interest: FID, flight distance, and flight angle. In cases in which the final model included species as a predictor term, models were selected for each species as well.

Initial analysis of the 2007-2009 data indicated the possibility that a few points had unusually high leverage in linear regression. The interquartile range was calculated for each variable and any record in which any individual measurement was above the third quartile plus one and a half times the IQR or below the first quartile minus one and a half times the IQR was excluded, creating a second dataset. A third dataset was created using the same procedure but first separating the data by species.

Model selection was run twice, once using the full dataset and once using the smaller cropped dataset appropriate to the model. Any term which was selected for the models using both datasets was included in the final model. Additionally, the measures of temperature were grouped as were the difference in height between vegetation at the flush and landing sites so that if both models selected a measure from that group the final model would include the measure selected by the model using the full dataset.

The final models were run with the GLM procedure. Individual means of categorical terms were then compared using Tukey tests at an alpha level of 0.05.

Testing for normality and a population mean of zero was performed with the UNIVARIATE procedure. This procedure performs three tests for a population mean of zero: Student's T, sign, and signed rank. The procedure also performs three tests for normality: Kolmogorov-Smirnov, Cramer-von Mises, and Anderson-Darling.

The REG procedure was used in testing when all variables were continuous.

Testing on the 2010 data, which included lengths, sexes, and colors of specimens, was performed in a similar manner. The GLMSELECT procedure was used to select optimal models using AIC as a selection criterion. Models were selected that predicted FD and FID both across all species and individually for each species. Selected models were then analyzed using the GLM procedure. The REG, CHART, and BOXPLOT procedures were used to create graphical comparisons between a number of variables and inform the interpretation of the model.

Phylogenetic Analysis

A phylogenetic tree with all nine study species was compiled from papers by Fries (2007), Song (2008), Litzenberger and Chapco (2001), and Chapco (1997). For any given variable a series of nearest-neighbor distances could be determined. Branch lengths were left undetermined, and so a species could have two nearest-neighbor branches. Nearest-neighbor branches could potentially split further into several species, although the largest number of nearest-neighbor species was three for *Hippiscus ocelote*. If a branch split into several species the branch was given a value equivalent to the average value for the variable of interest for the species on that branch. The nearest-neighbor distance was the absolute value of the difference between the value assigned to a species and the average of the values assigned to its nearest-neighbor branches. Smaller nearest-neighbor distances indicated that the variable of interest was more closely linked to phylogeny.

To analyze a variable a Monte Carlo simulation was run in R in which the values for each of the nine species was randomly reassigned on the phylogenetic tree 100,000 times and the sum of the nearest-neighbor differences calculated each time. The histogram of sums generated in this fashion defines a probability distribution for the sum of nearest-neighbor differences under the condition that phylogeny is entirely uncorrelated with the variable of interest.

RESULTS

Number of samples

A total of 297 grasshoppers was observed attempting escape between 2007 and 2009. For all species, 30 or more individuals were observed. Species for which more than 30

individuals were observed included *Syrbula admirabilis* (32 individuals), *Schistocerca americana* (40 individuals), *Hippiscus ocelote* and *Melanoplus femurrubrum* (33 individuals each), *Dichromorpha viridis* (34 individuals), and *Chortophaga viridifasciata* (35 individuals).

In 2010 three species of grasshoppers were targeted and captured: *Melanoplus femurrubrum*, *M. differentialis*, and *Syrbula admirabilis*. One hundred individuals of each *Melanoplus* species were captured. The scarcity of *Syrbula admirabilis* in 2010 resulted in only 83 individuals being captured.

Escape Angle

The angle between the flusher's approach path and the grasshopper's escape path was normally distributed. Only for *Spharagemon cristatum* did more than one test for normality give a significant *p*-value at the 0.05 level, and in that case all three did. The average escape angle of all species fell between 124.8° and 135.9°, and appeared to fall into a slightly left-skewed distribution when graphed.

The differences in escape angle between species were not significant, and angle did not have any significant correlation with any other variable.

FID: All species

FIDs were normally distributed for most species. The two exceptions were *Melanoplus differentialis* and *Dissosteira carolina*. In the case of *M. differentialis* this may be because it had a very low FID, and the left tail of the distribution would have had to have been less than zero to create a normal curve. For *D. carolina* the presence of an outlier was initially suspected, but its removal did not make the variable normal.

FID showed differences between species (p-value <0.0001) in a model without other terms. FID also showed clear differences between species in a model that included flight distance and the difference in the average height of vegetation at the flush and landing locations. *Dichromorpha viridis* had the shortest FID and was distinct from all but the two *Melanoplus* species and *Hippiscus ocelote*. These three species, along with *Chortophaga viridifasciata*, had intermediate FIDs and could not be distinguished from one another in this analysis. *Dissosteira carolina*, *Spharagemon cristatum*, and *Schistocerca americana* had the longest FIDs, and were not distinguishable from one another in that attribute. *D. carolina* was not distinguishable from *Hippiscus ocelote* or *Chortophaga viridifasciata* in this analysis, but the other two species differed from all but the other two species with long-FID (Table 3.1).

FID and FD were positively correlated with a high R-squared value of 0.3853. This correlation resulted in an exact match between lists of the average FID for each species ordered by magnitude and lists of the average FD for each species ordered by magnitude (Table 3.3).

FID was also correlated with the difference in the average height of vegetation at the flush and landing locations where movement from shorter vegetation to taller vegetation correlated to a longer FID. While the p-value was 0.0051 the R-squared value was 0.0507 indicating little real influence of this effect.

The average body length (head to wing tips) for each species and its average FID were positively correlated with a p-value of 0.0143. Average body lengths ranged from 21mm to 56mm.

FID: by species

Hippiscus ocelote and *Dichromorpha viridis* both showed correlations between FID and FD, both positively as in the model for all species. With other effects removed the FID - FD correlations expanded to include *Chortophaga viridifasciata* ($p=0.0143$), *Schistocerca americana* ($p=0.0045$), *Spharagemon cristatum* ($p<0.0001$), and, marginally, *Melanoplus femurrubrum* ($p=0.0680$). All of these correlations are also positive.

Within the 2010 data one species, *Syrbula admirabilis*, showed a correlation between FID and sex with males having longer FIDs than did females. While females of the species are approximately 1.5 times longer than males in this species sex was a better predictor of FID than was body length.

To examine the effect of size on FID while controlling for possible sex-linked differences in escape behavior the two closely-related species from the genus *Melanoplus* (Chapco et al., 1999) were also compared. The combined range of body lengths (head to wingtips) for the two species is 22mm to 46mm with large individuals of the smaller species (*M. femurrubrum*) being larger than the small individuals of the large species (*M. differentialis*). The size-FID relationship was not significant for any measurement of size.

Flight Distance

FD was not normally distributed for five species: *Chortophaga viridifasciata*, *Dichromorpha viridis*, *Dissosteira carolina*, *Melanoplus femurrubrum*, and *Syrbula admirabilis*. The remaining species all showed normal distributions on two or more tests for normality. The five species that did not have normally-distributed FDs were examined for

bimodality, as grasshoppers may escape by either jumping or flying. No evidence of bimodality was detected for any species.

FD showed a clear species effect in a model without other terms (p-value <0.0001). FD also showed clear differences between species in an analysis that included the FID and the daily average temperature as potential covariates. The four species with the shortest FDs, the two *Melanoplus* species, *Dichromorpha viridis*, and *Syrbula admirabilis* formed a group. *Melanoplus femurrubrum* was additionally indistinguishable from *Hippiscus ocelote* and *Chortophaga viridifasciata*. *Hippiscus ocelote*, *Chortophaga viridifasciata*, and *Spharagemon cristatum* grouped together with intermediate FDs. *Dissosteira carolina* and *Schistocerca americana* had the longest FDs and were distinguishable from all but each other (Table 3.2).

FD was correlated to FID as mentioned above. The correlation between FD and average daily temperature showed a negative slope and a very low R-squared value (0.0112), indicating low biological relevance.

The average body length of each species and its average FD were positively correlated with a p-value of 0.0097. Average body lengths ranged from 21mm to 56mm.

Flight Distance: by species

As discussed earlier both *Hippiscus ocelote* and *Dichromorpha viridis* showed correlations between FID and FD. *Schistocerca americana* also showed a slight positive correlation between daily average temperature and FD, with an R-squared of 0.1995. Both *Spharagemon cristatum* and *Syrbula admirabilis* showed correlations between FD and the average height of vegetation at their landing site. For *Spharagemon* the correlation was

positive with an R-squared of 0.2999. For *Syrbula* the correlation was negative with an R-squared of 0.1844.

Within the 2010 data only one species, *Melanoplus differentialis*, showed a correlation between body length and FD. These correlations had opposite slopes with different body length measures, however, and very low R-squared values (both <0.04) which brings into question the relevance of body length to FD in this species.

Within *Syrbula admirabilis*, which has distinct color morphs, FD was also linked to color. Green individuals flew shorter distances than did brown or mixed-color individuals and could be statistically distinguished from them in post-hoc Tukey testing. Very dark brown animals, classed as black, could not be statistically distinguished from green animals in this analysis. While green animals are always female (although not all females are green) this pattern is explained better by color than by sex.

In *Melanoplus femurrubrum* the average male flight distance was longer than the average female flight distance regardless of body size effects.

In the genus *Melanoplus* the size-FD relationship was negative using both measurements of lengths and not significant for mass.

Phylogeny

The sum of nearest-neighbor distances for FID was shorter than 90.8% of the distances generated in the Monte Carlo simulation. FDs showed a similar pattern with the true value being shorter than 93.7% of the Monte Carlo distances. Head-to-wingtip body length had a true value shorter than 96.7% of the Monte Carlo distances.

DISCUSSION

My data support the concept of species-specific FIDs and FDs for the grasshopper species examined. To the best of my knowledge this is the first demonstration of species-specific FIDs or FDs in an invertebrate taxon.

Species-specific FIDs and FDs were highly correlated with each other and FID and FD were correlated within some species as well. This is consistent with observations made by Clark (1948) on grasshoppers and an increase in both FID and FD was observed in Cooper (2006) when grasshoppers were subjected to multiple approaches. More generally, higher levels of threat have been observed to provoke more costly escape attempts in other species (Walther, 1969; Bonenfant and Cramer, 1996) and are correlated with longer FIDs in a number of studies (Rand, 1964; Bonenfant and Cramer, 1996; Cooper, 1997; Smith, 1997; Hemmi, 2005). However, Ydenberg and Dill's (1986) economic model links FID to both threat level and escape cost. Escape distance is expected to increase as the cost of escaping per unit distance decreases.

Differentiating between perceived-risk and lowered-cost explanations for the FID-FD link within a single species would be nearly impossible without much more extensive research into how grasshoppers analyze threat. Between species, however, the perceived-threat hypothesis becomes much harder to support. Within a single species it is reasonable to suggest that an individual that perceives the approaching researcher as a more dangerous predator will flee earlier and flee farther. This implicitly assumes that each individual has the same ability to flee and that fleeing further represents an individual utilizing more of that capacity, prompted by an evaluation of more serious threat. Between species the assumption

of equal flight capacity is unfounded. One species in this study, *Dichromorpha viridis*, is brachypterous in most individuals while other species (notably *Dissosteira carolina*, *Spharagemon cristatum*, and *Schistocerca americana*) are capable of long, fast flights. Equal threat levels to a non-volant *Dichromorpha* and a volant *Schistocerca* should not be expected to produce equal flight responses.

If, instead, FID and FD are positively correlated because the cost of flight varies between species this would explain both interspecific and intraspecific trends. In this case *Schistocerca americana* has the longest average FID because its cost of escaping is the lowest of the nine species studied and so it loses the least by escaping early, and the low cost of flight also results in the longest average FD.

It is also possible that these two hypotheses work together over evolutionary time and so species which evolve defenses other than flight are less likely to evolve the capacity for sustained, rapid flight as in Goodman (2009) where lizards in open habitats without alternate defenses were found to have longer legs. These species would also be expected to regard predators as less threatening because of their additional defenses. This hypothesis is generally supported by the linkage between color morph and flight distance in *Syrbula admirabilis*. Since temperature was not found to be important in predicting flight distance for this species the differences in heat absorption of the different color morphs should be irrelevant to their escape characteristics (Forsman, 1997). Instead, these differences are probably another example of more cryptic prey investing less energy in escape (Heatwole, 1968; Martin et al., 2009; Cuadrado et al., 2001; Cooper et al., 2008; Cabido et al., 2009) or of the effectiveness of escape behavior varying with color phase as in the grasshopper *Tetrix*

subulata (Forsman and Appelqvist, 1998). In either case the additional defenses of some color morphs of *S. admirabilis* would be linked to a lower investment in escape.

FID and FD are both closely correlated with phylogeny. The mechanism for this correlation is unclear. One potential mechanism is body size which was found to be closely correlated to phylogeny in this study. In several other species escape behavior is related to body size (Smith, 1997; Cuadrado et al., 2001; Blumstein et al., 2005; Dangles et al., 2007) but body size was not consistently correlated with either FID or FD in this study.

When data from all species were used, a positive correlation between body size and both FID and FD was found. However, different results were obtained when the data used were from more phylogenetically restricted sets of grasshoppers. *Syrbula admirabilis* is highly sexually dimorphic and within this species smaller males flushed earlier than larger females. In the genus *Melanoplus* larger individuals flew less distance than did smaller ones. Neither species of *Melanoplus* showed a significant and consistent trend between size and FID or FD on its own. Because these apparent size effects are not consistent in direction or significance, size is not a good explanation for the variability in species-specific FIDs and FDs.

Other potential mechanisms for the correlation between phylogeny and FID and FD include ecological factors that may also be correlated with phylogeny. One important ecological factor is habitat choice which influences the number and type of predators encountered and the ability of predator and prey to detect one another (Amo et al., 2007). Habitat choice may also influence that ability of a grasshopper to conceal itself. Other candidates for the correlation between phylogeny and FID and FD are alternate defenses such

as spiny tarsi or chemical defenses (Despland, 2005). Additional studies are needed to determine the mechanism whereby escape behavior is phylogenetically conserved. Work on other invertebrate taxa would also help determine whether phylogenetic conservatism of escape behavior is common in invertebrates.

LITERATURE CITED

- Amo, L., Lopez, P., & Martin, J. (2007). Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. *Canadian Journal of Zoology*, 85(6), 743-751.
- Anderson, D. J., Budde, C., Apanius, V., Gomez, J. E. M., Bird, D. M., & Weathers, W. W. (1993). Prey size influences female competitive dominance in nestling American kestrels (*Falco sparverius*). *Ecology*, 74(2367-376).
- Balgooyen, T. G. (1997). Evasive mimicry involving a butterfly model and grasshopper mimic. *American Midland Naturalist*, 137(1), 183-187.
- Blumstein, D. T. (2003a). Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? *Biological Conservation*, 110, 97-100.
- Blumstein, D. T. (2003b). Flight initiation distance in birds is dependent on intruder starting distance. *Journal of Wildlife Management*, 67, 852—857.
- Blumstein, D. T., Fernandez-Juricic, E., Zollner, P. A., & Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, 42(5), 943-953.
- Bonenfant, M., & Kramer, D. L. (1996). The influence of distance to burrow on flight initiation distance in the woodchuck, *Marmota monax*. *Behavioral Ecology*, 7, 299-303.
- Broom, M., & Ruxton, G. D. (2005). You can run — or you can hide: optimal strategies for cryptic prey. *Behavioral Ecology*, 16, 534-540.
- Cabido, C., Galan, P., Lopez, P., & Martin, J. (2009). Conspicuousness-dependent antipredatory behavior may counteract coloration differences in Iberian rock lizards. *Behavioral Ecology*, 20(2), 362-370.

- Chapco, W., Martel, R., & Kuperus, W. (1997). Molecular phylogeny of North American band-winged grasshoppers (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 90(5), 555-562.
- Chapco, W., Kuperus, W. R., & Litzenberger, G. (1999). Molecular phylogeny of melanopline grasshoppers (Orthoptera: Acrididae): The genus *Melanoplus*. *Annals of the Entomological Society of America*, 92(5), 617-623.
- Clark, E. J. (1948). Studies in the ecology of British grasshoppers. *Transactions of the Royal Entomological Society of London*, 99, 173-222.
- Cooper Jr, W. E., & Cooper, W. E. J. (1997). Factors affecting risk and cost of escape by the broad-headed skink (*Eumeces laticeps*): predator speed, directness of approach, and female presence. *Herpetologica*, 53, 464-474.
- Cooper, W. E. (2006). Risk factors and escape strategy in the grasshopper *Dissosteira carolina*. *Behaviour*, 143(10), 1201-1218.
- Cooper, W. E., Caldwell, J. P., & Vitt, L. J. (2008). Effective crypsis and its maintenance by immobility in *Craugastor* frogs. *Copeia*, (3), 527-532.
- Cuadrado, M., Martin, J., & Lopez, P. (2001). Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biological Journal of the Linnean Society*, 72(4), 547-554.
- Dangles, O., Pierre, D., Christides, J. P., & Casas, J. (2007). Escape performance decreases during ontogeny in wild crickets. *Journal of Experimental Biology*, 210(18), 3165-3170.
- Despland, E. (2005). Diet breadth and anti-predator strategies in desert locusts and other orthopterans. *Journal of Orthoptera Research*, 14(2), 227-233.
- Fernandez-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, 80(7), 1212-1220.
- Forsman, A., & Appelqvist, S. (1998). Visual predators impose correlational selection on prey color pattern and behavior. *Behavioral Ecology*, 9(4), 409-413.
- Forsman, Anders. (1997). Thermal capacity of different colour morphs in the pygmy grasshopper *Tetrix subulata*. *Annales Zoologici Fennici* (Vol. 34, pp. 145-149).
- Fries, M., Chapco, W., & Contreras, D. (2007). A molecular phylogenetic analysis of the Oedipodinae and their intercontinental relationships. *Journal of Orthoptera Research*, 16(2), 115-125.

- Frix, M. S., Hostetler, M. E., & Bildstein, K. L. (1991). Intrapsecies and interspecies differences in responses of Atlantic sand (*Uca pugilator*) and Atlantic marsh (*U. pugnax*) fiddler-crabs to simulated avian predators. *Journal of Crustacean Biology*, 11(4), 523-529.
- Giles, L. W. (1940). Food habits of the raccoon in eastern Iowa. *The Journal of Wildlife Management*, 4(4), 375-382.
- Goodman, B. A. (2009). Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. *Journal of Evolutionary Biology*, 22(7), 1535-1544.
- Gutzwiller, K. J., & Marcum, H. A. (1997). Bird reactions to observer clothing color: implications for distance-sampling techniques. *Journal of Wildlife Management*, 61, 935-947.
- Hamilton W. J., J. (1951). The food of the opossum in New York state. *The Journal of Wildlife Management*, 15(3), 258-264.
- Heatwole, H. (1968). Relationship of escape behavior and camouflage in anoline lizards. *Copeia*, 1968, 109-113.
- Hemmi, J. M. (2005). Predator avoidance in fiddler crabs: 1. Escape decisions in relation to risk of predation. *Animal Behaviour*, 69, 603-614.
- Hockman, J. G., & Chapman, J. A. (1983). Comparative feeding habits of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) in Maryland. *American Midland Naturalist*, 110(2), 276-285.
- Joern, A. (1988). Foraging Behavior and switching by the grasshopper sparrow *Ammodramus* *savannarum* searching for multiple prey in a heterogeneous environment. *American Midland Naturalist*, 119(2), 225-234.
- Kennedy, C. H. (1950). The relation of american dragonfly-eating birds to their prey. *Ecological Monographs*, 20(2), 103-142.
- Lindsey, A. (1939). Food of the starling in Central New York State. *Wilson Bulletin*, 51(3), 176-182.
- Litzenberger, G., & Chapco, W. (2001). A molecular phylogeographic perspective on a fifty-year-old taxonomic issue in grasshopper systematics. *Heredity*, 86(1), 54-59.

- Martin, J., Luque-Larena, J. J., & Lopez, P. (2009). When to run from an ambush predator: balancing crypsis benefits with costs of fleeing in lizards. *Animal Behaviour*, 78(4), 1011-1018.
- Nicholson, W. S., Hill, E. P., & Briggs, D. (1985). Denning, pup-rearing, and dispersal in the gray fox in East-Central Alabama. *The Journal of Wildlife Management*, 49(1), 33-37.
- Pinkowski, B. C. (1978). Feeding of nestling and fledgling Eastern bluebirds. *The Wilson Bulletin*, 90(1), 84-98.
- Rand, A. S. (1964). Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology*, 45, 863-864.
- Smith, D. G. (1997). Ecological factors influencing the antipredator behaviors of the ground skink, *Scincella lateralis*. *Behavioral Ecology*, 8(6), 622-629.
- Song, H., & Wenzel, J. W. (2008). Phylogeny of bird-grasshopper subfamily Cyrtacanthacridinae (Orthoptera: Acrididae) and the evolution of locust phase polyphenism. *Cladistics*, 24(4), 515-542.
- Walther, F. R. (1969). Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, 34, 184-221.
- Ydenberg, R. C., & Dill, L. M. (1986). The economics of fleeing from predators. *Advances in the Study of Behavior*, 16, 229-249.

Table 3.3. The FID and flight distances of grasshoppers listed by the average for each species. The species are listed in ascending order for both distances. Refer to Tables 3.1 and 3.2 for statistical comparisons of the differences between species.

Species	Mean FID (cm)	Mean Flight Distance (cm)
<i>Dichromorpha viridis</i>	12	62
<i>Syrbula admirabilis</i>	13	98
<i>Melanoplus differentialis</i>	18	126
<i>Melanoplus femurrubrum</i>	20	177
<i>Hippiscus ocelote</i>	39	362
<i>Chortophaga viridifasciata</i>	49	373
<i>Spharagemon cristatum</i>	69	517
<i>Dissosteira carolina</i>	69	774
<i>Schistocerca americana</i>	82	1088

CHAPTER FOUR

A QUANTATIVE INVESTIGATION OF GRASSHOPPER CAMOUFLAGE

INTRODUCTION

Camouflage is important for the survival of many species. However, it is not without costs. The coloration of a cryptic prey species must strike a balance between thermoregulation, intraspecific signaling, and crypsis (Endler, 1978) and perhaps mechanical, UV-protective, and immune functions of certain pigments (Averill, 1923; St Leger et al., 1988; Hajek and St Leger, 1994; Gunn, 1998; Majerus 1998; Wilson et al., 2001; Goldstein et al., 2004). Camouflage is also only one of many defenses most animals possess and may not always be a particularly important part of an animal's overall defense. Movement actually negates much of the value of camouflage (Ioannou and Krause, 2009) and so species that depend on frequent movement for defense or other biological functions may have little to gain from camouflage.

Because of the cost of being camouflaged, variation in overall levels of camouflage between species is to be expected. The causes of this variation are of more interest. The use of color for camouflage can be broadly broken into chromatic background matching and disruptive camouflage (Cott, 1940). Fraser et al. (2007) has found that people hunting for artificial moths on a computer screen could find even disruptively-colored moths if they matched their background in tone poorly. However, many species live in heterogeneous habitats without one single background color or color pattern. In a sufficiently heterogeneous background crypsis will not be possible in all areas of the habitat (Merilaita et al., 1999; Merilaita et al., 2001). In these habitats disruption, which is theoretically less background-dependent than chromatic matching, may be the optimal strategy. Ahnesjö and Forsman (2006) found that striped morphs of the polymorphic grasshopper *Tetrix undulata* were less

choosy about the background color to which they retreated when disturbed than were their self-colored conspecifics which they suggest is because stripes serve as disruptive camouflage regardless of the grasshopper's background. Obviously, choice of background is another mechanism by which functional crypsis can be enhanced or degraded as the choice of an incorrect background can destroy the effectiveness of any crypsis.

Grasshoppers have been used to study crypsis since serious study of the phenomenon began (Poulton, 1890). Many species of grasshoppers appear cryptic to the human eye and studies have demonstrated that crypsis has survival value for grasshoppers (Isely, 1938; Gillett and Gonta, 1978; Forsman and Appelqvist, 1998). Color morph frequencies in some species appear to be correlated with color in the natural environment (Otte and Williams, 1972) while in other cases this correlation has not been found or is weak (Unsicker et al., 2008; Tsurui et al., 2010). Notably, this correlation is supported in two species which can switch between color morphs during their lifetime in response to environmental factors and it is weakly supported or not supported in two species that have genetically fixed color morphs (Karlsson et al., 2010). Some species of grasshopper can also change color to match their background over the space of several days (Rowell, 1971). Several studies have also found that grasshoppers prefer backgrounds that match their own color, especially when the grasshopper has just been disturbed (Gillis, 1982; Calver and Bradley, 1991; Eterovick et. al., 1997; Ahnesjö and Forsman, 2006).

The color of grasshoppers has been shown to be important for thermoregulation in some species (Forsman, 1997; Fielding and Defoliart, 2005) and some species also use

intraspecific signals that involve brightly-colored body regions (Niedzlek-Feaver, 1995; Ostrowski et al., 2009).

Given the trade-offs involved in camouflage it is worth investigating the degree to which various species are camouflaged and the methods they use to attain this level of camouflage. This requires quantifying camouflage. Fraser et al. (2007) used a computer program to score human observers in their attempts to locate digital moths, thus quantifying the camouflage of the moths. Similar systems can potentially be used to quantify the camouflage of real species in their natural environments.

In this study I used digital photographs of grasshoppers against their natural backgrounds to quantify their relative levels of crypsis. None of the species used were known or suspected to be mimetic or aposematic. Several species were polymorphic for color allowing direct comparisons between color morphs. Both self-colored and heavily-patterned (potentially disruptively camouflaged) species were included in the study.

METHODS

Photographs

Between 2007 and 2009 I took 723 photographs of grasshoppers in the Lake Wheeler Farm Unit fields, with a Canon Powershot A540 digital camera. Grasshoppers were photographed when and where they were encountered, although grasshoppers that were encountered on man-made substrate were excluded. Photographs were taken at various locations in proportion to the grasshopper population present there and every effort was made to secure photographs from multiple locations. Grasshoppers were photographed with their wings closed and the view of their bodies mostly unobstructed by vegetation. The angle of

the grasshopper in the photograph was further randomized by alternately taking the photograph from the initial angle of approach, from 90 degrees to the right, from 90 degrees to the left, and from 180 degrees to the initial angle of approach.

Nine species of grasshoppers were photographed: *Dichromorpha viridis*, *Syrbula admirabilis*, *Schistocerca americana*, *Melanoplus femurrubrum*, *M. differentialis*, *Chortophaga viridifasciata*, *Hippiscus ocelote*, *Spharagemon cristatum*, and *Dissosteira carolina*. Color variants were treated separately: brown and green forms for *C. viridifasciata*, brown, green, and green-above brown-below (bicolored) forms for *D. viridis*, and brown, green, and black forms for *S. admirabilis*. Black forms are not always recognized as distinct for *S. admirabilis* but in this study they were visually differentiable from the brown form of which they are probably a darker variety.

From the initial set of 723 photographs thirty photographs were selected for each species and for each color morph of each polymorphic species. The main criterion for selection was the clarity of the photograph but some photographs were excluded because they were too small for the image processing in the next step.

All images were standardized in size and the location of the grasshopper within the photograph was randomized. Standardization and randomization were accomplished with the aid of an Excel spreadsheet. A body-length was calculated for each grasshopper (head to the end of the forewings or the abdomen, whichever was furthest) and the photograph was reduced in size to make the grasshopper 183 pixels in length. The x and y coordinates of the grasshopper's visual center were used to calculate a 550 x 550 pixel frame around the grasshopper. This frame was then offset both vertically and horizontally so that the

grasshopper's center was randomly repositioned within the frame, excluding a 5% margin on each side. This margin was calculated to prevent the grasshopper from extending out of the frame. If this occurred new random offsets were obtained until the grasshopper fit within the frame. The photograph was then cropped to the frame.

Upon upload to the final program ten blurred pictures were created from the in-focus images. Initial testing had been conducted to optimize the levels and methods of blurring. Applying a single level of blurring multiplied by 1-10 produced a more even change in the photographs than applying the same level 1-10 times. The level chosen was 0.25% of the width of the photograph.

Collection of Data

All finished photographs were loaded into a custom-written PHP web application (hereafter referred to as the viewing program) which presented users with sequences in a blurriest-to-clearest order. Each image in the sequence appeared on-screen for one second. The visual impression was that of a blurry picture coming into focus.

Users were presented with a short description of the task and some example photographs. They then attempted to find the grasshopper in each sequence. Users were allowed two clicks to find the grasshopper. The order in which sequences were presented was randomized.

Users logged in using unique IDs and passwords. If a user did not complete the entire task in one sitting (which most did not) the program remembered which sequences they had already viewed and presented them with only the remaining sequences when they next logged in.

The viewing program output consisted of several sections. Each record of output was individually identified by a number that counted the records. Each record was numbered individually and contained the user's IP address and a user ID number. The ID number of the photographic sequence was also included along with a number between one and 420 that recorded where in the overall sequence of pictures this photographic sequence had appeared for the user. The x and y coordinates of the first and second mouse clicks were recorded along with the time of the click in seconds. The time record was a proxy for the actual level of blurring being viewed so records were integers without rounding. If no click was recorded the coordinates -1, -1 were recorded and the time was recorded as twelve seconds (since the entire sequence finished in eleven seconds).

Analysis

A second set of photographs (hereafter referred to as the red-marked photographs) was created in which the grasshopper was colored red by hand. The shade of red chosen was unlike any color that occurred in the original photograph as verified by a program custom-written in Python 2.7. This allowed other programs to automatically determine whether a given pixel was part of the grasshopper or the background by checking the color of that pixel in the corresponding red-marked photograph.

A second custom-written Python program analyzed the color data for the original photographs. The red, green, and blue values of each pixel were acquired and an average red, green, and blue value was produced for the entire photograph, the background, and the grasshopper. Pixels were additionally classified by color using two different methods and pixel counts per color were generated for the entire photograph, the background, and the

grasshopper. This program also output the visible area of the grasshopper in pixels. This information was appended to the existing data for each photograph.

A third Python program matched each line of data from the viewing program to a particular photograph and used the data for each photograph and the red-marked photographs to determine at what point (if ever) the viewer correctly clicked on the grasshopper and created a large dataset containing the information for each click and the information for the selected photograph. This dataset was further analyzed using SAS 9.2.

Initially, a general linear model was used to predict the time of the first click on a grasshopper by its species and color morph (combined into a single variable hereafter referred to as color-species). Two more models were created, one which included user statistics (user ID and how many photographs the user had seen previously) while the other included the size of the grasshopper. These models investigated and corrected for the effect of non-target variables.

Finally, a general linear model was created that predicted the time it took a viewer to click on a grasshopper by the size of the grasshopper, user ID of the viewer, and the grasshopper's chromatic match to the background. Because previous analysis had shown that greenness of the background and the grasshopper was important a GLMSELECT procedure was run using AIC to select the best model terms. The difference in green levels between the background and the grasshopper outperformed the total summed color difference and so the greenness differences were used in the following model. Furthermore, the greenness statistics drawn from using a color classification meant to match human vision outperformed the other systems. The greenness match was calculated by taking the absolute

values of the differences between background and grasshopper counts of green pixels, each adjusted for the size of the area sampled. The residuals from this model were predicted by color-species, viewer, and visible area of the grasshopper in a general linear model in order to test for significant differences between pairs.

Each color-species was also tested for response to greenness by predicting the average search time per photo by the greenness of the background and the visible area of the grasshopper. The visible area of the grasshopper was not significant within any given color species and some color-species were best fit with a second-order polynomial regression on greenness. PROC GLM was used to find the p-values of each potential correlation and generate an R^2 value for the final model in which all terms were significant.

In all models pairwise comparisons were done with Tukey tests. The UNIVARIATE procedure was used to obtain some averages. The experiment-wide alpha level was 0.05.

RESULTS

There were 415 users, 276 of whom completed all 420 pictures. The dataset contained 129,295 entries..

Raw data

The color-species was a highly significant (p-value < 0.0001) predictor of the time it took a viewer to click on a grasshopper. Nearly all pairwise comparisons were significant (Table 4.1). In order from hardest-to-find to easiest-to-find the color species are:

Spharagemon cristatum, *Hippiscus ocelote*, brown *Syrbula admirabilis*, *Melanoplus femurrubrum*, brown *Chortophaga viridifasciata*, *M. differentialis*, green *S. admirabilis*,

bicolored *Dichromorpha viridis*, green *D. viridis*, *Dissosteira carolina*, brown *D. viridis*, green *C. viridifasciata*, *Schistocerca americana*, and black *Syrbula admirabilis*.

Adjusted models

The least squares means from the models adjusting for user data and for size differed from the raw data by an average of 1.6%. However, this was sufficient to change the relative ranks of several species by a small margin. The size-adjusted order of color species from hardest-to-find to easiest-to-find is: *Hippiscus ocelote*, *Spharagemon cristatum*, *Melanoplus femurrubrum*, brown *Syrbula admirabilis*, brown *Chortophaga viridifasciata*, green *Dichromorpha viridis*, *M. differentialis*, bicolored *D. viridis*, green *S. admirabilis*, brown *D. viridis*, *Dissosteira carolina*, green *C. viridifasciata*, *Schistocerca americana*, black *Syrbula admirabilis*.

Habitat and grasshopper coloration

Habitat coloration by color-species was divided into two distinct clusters, a green habitat cluster with an average green pixel percent ranging from 76-34% and a brown habitat cluster with average green pixel percents below 10% (Table 4.2). The brown color morph of *Syrbula admirabilis* was the only intermediate color-species, with 16% green pixels. The following species inhabited green habitats: black and green *Syrbula admirabilis*, all three color morphs of *Dichromorpha viridis*, *Schistocerca americana*, *Melanoplus differentialis*. The species inhabiting brown habitats were: both color morphs of *Chortophaga viridifasciata*, *Hippiscus ocelote*, *Melanoplus femurrubrum*, *Dissosteira carolina*, *Spharagemon cristatum*.

Grasshopper coloration was similarly bimodal although greenness scores were lower overall (Table 4.2). The four green or partly green species (the three green morphs and the bicolored morph of *Dichromorpha viridis*) ranged from a high score of 81% green pixels to a low of 20% green pixels. The remaining ten brown species had greenness scores below 3% of pixels. Only one species was intermediate, the very dark phase of *Syrbula admirabilis* which was 10% green. I suspect that this number is due to bleed-over of greens from the grasshopper's habitat as this animal is not at all green to look at but is very thin which promotes bleed-over.

Eight color-species had intraspecific responses to the greenness of the background (Table 4.3). Of these seven species, *Schistocerca americana*, bicolored *Dichromorpha viridis*, all three color morphs of *Syrbula admirabilis*, *Melanoplus differentialis*, and green *Chortophaga viridifasciata* had correlations graphically represented as parabolas with the extreme ends pointing down. One further color-species, the brown *D. viridis*, had a negative linear relationship to greenness. In no other color-species was a significant correlation detected. R^2 values ranged from 0.29 to 0.69 without apparent clustering. Parabolic maxima ranged from 0.19 to 0.58 given a possible range of 0 (no green in background) to 1 (a solid green background).

Color matching

Overall, color matching explained the variability in the time it took a viewer to locate a grasshopper well. Without other variables included a grasshopper that was entirely green on a non-green (i.e., brown) background (or vice versa) would be expected to be found 3.1

seconds before a grasshopper that matched its background perfectly in greenness (or brownness). The adjusted R^2 value for this relationship is 0.4983.

The residuals in the larger model including user ID and grasshopper size as well as greenness differences did not cluster well (Table 4.4). One group stuck out with the highest three residuals in absolute value. These species, *Dissosteira carolina*, *Schistocerca americana*, and green *Chortophaga viridifasciata*, all had negative residuals indicating that they were easier to find than would be expected from their greenness matching alone. All other species had positive residuals. The remaining species existed along a continuum of residual values (0.48 to 0.02) with a slightly larger gap between the eighth and ninth highest absolute value (0.30 to 0.15). The species with residuals more extreme than 0.15 were brown *Syrbula admirabilis*, *Hippiscus ocelote*, *Spharagemon cristatum*, green *Dichromorpha viridis*, and *Melanoplus differentialis*.

DISCUSSION

Species and color-morphs varied in crypsis and crypsis was largely predictable from the extent to which the grasshopper and the background matched in greenness. Some species did diverge from the estimations of the greenness-matching model, especially a small group of species that appeared to be less cryptic than the model estimated.

Three species in the study were relatively un-patterned: *Melanoplus differentialis*, which always has black markings on the legs and occasionally also has them on the head or thorax but is mostly a single solid color, *Dichromorpha viridis* which has two self-colored morphs (as well as a third morph with noticeable patterning), and *Dissosteira carolina* which has occasional light spotting. *M. differentialis* and brown *Dichromorpha viridis* both inhabit

very green habitats and their camouflage is estimated well by the greenness-matching model. Green *Dichromorpha viridis*, which favor a very green background, are more cryptic than estimated by the model. *Dissosteira carolina* is found on much browner habitats and underperforms the model's expectations more dramatically than any other species.

The remaining morph of *Dichromorpha viridis* and both green and brown forms of *Chortophaga viridifasciata* have color patterns composed of large blocks of color. In *D. viridis* the bicolored morphs has a green dorsal surface and is otherwise brown. In *C. viridifasciata* both morphs tend to have black on the tegmina, almost always at the tips and sometimes across the entire tegman. The bicolored morph of *D. viridis* inhabited a very green habitat and matched the model's estimations of its crypsis well. The brown morph of *C. viridifasciata* also matches the model's estimations well but is a brown species that lives on a brown habitat.

Green *C. viridifasciata* fits the greenness model poorly. It is much easier to find than expected. It also matches its habitat poorly. When the data from each picture are examined green *C. viridifasciata* are maximally camouflaged on a 23% green background but their average background is only 9% green.

The remaining species have distinct patterns. *Melanoplus femurrubrum* and *Spharagemon cristatum* have bars and blotches of black that cut across parts of their bodies. Both are brown grasshoppers that favor brown backgrounds. *M. femurrubrum* fits the greenness-matching model well while *S. cristatum* outperforms it noticeably.

Syrbula admirabilis, *Schistocerca americana*, and *Hippiscus ocelote* are all covered in dense patterns of light and dark. In *Schistocerca americana* and *Hippiscus ocelote* these

patterns do not vary much in density. In *Syrbula admirabilis* individuals may be more or less heavily patterned. *H. ocelote* and the brown form of *S. admirabilis* over-perform the greenness-matching model to a higher degree than do any other species. The other two morphs of *Syrbula admirabilis* do not differ from the model's estimations by much, and *Schistocerca americana* is the second-worst underperformer. *Schistocerca americana* (which are brown) and green and black *Syrbula admirabilis* are all found most frequently on green backgrounds. Brown *Syrbula admirabilis* are found in intermediate habitat, and *Hippiscus ocelote* (which are brown) are found in brown habitat.

Within *Syrbula admirabilis* some additional observations can be made. Black animals simply match their green background extremely poorly. Very little can be said about them but both green and brown animals show some variation in the amount of time required to locate them. When I examined the eight easiest-to-find brown *Syrbula* (average time to find them was under eight seconds) they were all either individuals with light patterns or oriented to the light or camera so that their patterns were indistinct. Conversely, the nine hardest-to-find animals (average time to find them was over ten-and-a-half seconds) were more strongly patterned and often visually bisected or trisected by dark or light markings. For the green *Syrbula* no such pattern existed. Instead, the easiest-to-find animals (eleven animals with an average time to find them under eight seconds) were noticeable primarily because they had all chosen to position themselves in the middle of large brown patches of earth or dead vegetation.

Four species or color-morphs deserve some additional consideration. Black *Syrbula admirabilis* are effectively non-cryptic. Since only males seem to darken to this color it is

possible that black male *Syrbula* gain an advantage in mating either through female choice or, perhaps more likely, because they may be able to warm up more quickly than their lighter conspecifics and reach receptive females first.

Green *Chortophaga viridifasciata* are also unusually easy to see although this time in comparison to the brown morph of the same species. Several possibilities exist to explain this. One is that green and brown morphs do not have different habitat preferences. Indeed, the average greenness of the habitats they were found on differs by 0.23% of the total range and brown *Chortophaga* are found on the greener backgrounds. By contrast, green and brown *Dichromorpha* differ in background-greenness by 11.48% and green and brown *Syrbula* differ in background-greenness by 23.34%, both in the expected direction. It is also possible that a green animal on a brown background is more noticeable to the human eye than a brown animal on a green background, especially when one considers that green backgrounds are vegetated and therefore full of complex shapes to distract the eye.

Schistocerca americana is also an odd underperformer, especially because it is often quite difficult to locate visually in the field. It is not uncommon to watch a *Schistocerca* land and yet be unable to locate the animal despite the fact that it may later fly up from the location that was searched. It is possible that *Schistocerca* relies on diving beneath the grass where its spots and stripes might provide better camouflage and that because this study excluded photos in which the animal was significantly obscured by vegetation this aspect of its crypsis was overlooked. However, several other possibilities exist. One is that *Schistocerca*, a very strong flier, positions itself in areas that are good for takeoff when pursued and that these locations are not areas where its color patterns are especially cryptic.

This may be combined with the previous hypothesis in which case *Schistocerca* might have two modes of escape only one of which, the non-cryptic one, was tested here. It is also possible that *Schistocerca* is adapted to be camouflaged in its winter habitat. Since it is the only grasshopper in the region that overwinters as an adult it may be under extremely high predation pressure during this season. Since an animal should optimize crypsis for the habitat in which it is most at risk (Endler, 1978) it is possible that *Schistocerca* is well-camouflaged in winter but not during summer.

Finally, the pair of species *Dissosteira carolina* and *Spharagemon cristatum* deserve consideration. *D. carolina* underperforms the greenness-matching model's estimations while *S. cristatum* over-performs. The species are closely related (Chapco, 1997) and very similar in appearance. The only noticeable difference in coloration is that *S. cristatum* is much more likely to have bands or blotches on its body. If disruptive coloration is important to the camouflage of grasshoppers these results would make sense.

Overall, this study indicates that chromatic matching is more important than disruption, much as found by Fraser et al. (2007). The utility of the greenness-matching model which does not include disruptive patterning is the best evidence for this difference. Additional evidence comes from the examination of mis-clicks where users clicked on what they falsely believed to be grasshoppers. These clicks were almost entirely absent from photographs in which grasshoppers did not match their background in color. It was only when the grasshopper matched its background chromatically that users began to click on objects that were shaped roughly like grasshoppers and in these cases they favored objects that did not match the background color well.

However, the value of chromatic matching is not constant across all habitats. The absolute value of the residual from the greenness-matching model tends to increase, as does its variance, as the background the species favors becomes less green. One hypothesis that may explain this is that disruptive camouflage may have greater utility in brown habitats than in green ones. Green backgrounds are, in this study, inherently heterogeneous since they are composed of multiple plants. While some brown backgrounds are composed of many small rocks, twigs, or dead plants others are simple expanses of dirt. Detecting the shape of a grasshopper against a background of other three-dimensional shapes is presumably more difficult than detecting the shape of a grasshopper against a flat background. This may mean that in a green background the detection of a grasshopper by shape alone is a difficult task that will occur slowly while on a brown background it may happen much faster unless disruptive patterns break up that shape. In a vegetated background the disruption of edges is also much more likely to occur by the partial occlusion of the grasshopper by plant material than it is in an un-vegetated background. Despite this, chromatic matching remains more important than disruption in every color of habitat.

LITERATURE CITED

- Ahnesjoe, J., & Forsman, Anders. (2006). Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance. *Evolutionary Ecology*, 20(3), 235-257.
- Averill, C. K. (1923). Black wing tips. *Condor*, 25(2), 57-59.
- Calver, M. C., & Bradley, J. S. (1991). Can microhabitat selection explain sex-related colour morph frequencies in the grasshopper *Acrida conica* Fabricius? *Animal Behaviour*, 41(6), 1101-1102.

- Chapco, W., Martel, R., & Kuperus, W. (1997). Molecular phylogeny of North American band-winged grasshoppers (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 90(5), 555-562.
- Cott, H. B. (1940). *Adaptive coloration in animals*. London, UK: Methuen.
- Endler, J. A. (1978). A predator's view of animal color patterns. *Evolutionary Biology*, 11, 319-364.
- Eterovick, P. C., Figueira, J. E. C., & Vasconcellos-Neto, J. (1997). Cryptic coloration and choice of escape microhabitats by grasshoppers (Orthoptera: Acrididae). *Biological Journal of the Linnean Society*, 61, 485-499.
- Fielding, D. J., & Defoliart, L. S. (2005). Density and temperature-dependent melanization of fifth-instar *Melanoplus sanguinipes*: interpopulation comparisons. *Journal of Orthoptera Research*, 14(1), 107-113.
- Forsman, A., & Appelqvist, S. (1998). Visual predators impose correlational selection on prey color pattern and behavior. *Behavioral Ecology*, 9(4), 409-413.
- Forsman, Anders. (1997). Thermal capacity of different colour morphs in the pygmy grasshopper *Tetrix subulata*. *Annales Zoologici Fennici* (Vol. 34, pp. 145-149).
- Fraser, S., Callahan, A., Klassen, D., & Sherratt, T. N. (2007). Empirical tests of the role of disruptive coloration in reducing detectability. *Proceedings of the Royal Society B Biological Sciences*, 274(1615), 1325-1331.
- Gillett, S. D., & Gonta, E. (1978). Locust as prey: Factors affecting their vulnerability to predation. *Animal Behaviour*, 26(1), 282-289.
- Gillis, J. E. (1982). Substrate colour-matching cues in the cryptic grasshopper *Circotettix rabula rabula* (Rehn & Hebard). *Animal Behaviour*, 30(113-116), 113-116.
- Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M., & Burt Jr., E. H. (2004). Bacterial degradation of black and white feathers. *The Auk*, 121(3), 656-659.
- Gunn, A. (1998). The determination of larval phase coloration in the African armyworm, *Spodoptera exempta* and its consequences for thermoregulation and protection from UV light. *Entomologia Expis Applicata*, 86, 125-133.
- Hajek, A. E., & St Leger, R. J. (1994). Interactions between fungal pathogens and insect hosts. *Annual Review of Entomology*, 39, 293-322.

- Ioannou, C. C., & Krause, J. (2009). Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biology Letters*, 5(2), 191-193.
- Isely, F. B. (1938). Survival value of acridian protective coloration. *Ecology*, 19(3), 370-389.
- Karlsson, M., & Forsman, Anders. (2010). Is melanism in pygmy grasshoppers induced by crowding? *Evolutionary Ecology*, 24(5), 975-983.
- Majerus, M. E. N. (1998). *Melanism* (pp. 28-29). New York: Oxford University Press.
- Merilaita, S., Lyytinen, A., & Mappes, J. (2001). Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B: Biological Sciences*, 268(1925–1929).
- Merilaita, S., Tuomi, J., & Jormalainen, V. (1999). Optimisation of cryptic coloration in heterogeneous habitats. *Biological Journal of the Linnean Society*, 67(151–161).
- Niedzlek-Feaver, M. (1995). Crepitation, pair formation, and female choice in *Chortophaga viridifasciata* (DeGeer) (Orthoptera: Acrididae). *Journal of Orthoptera Research*, 4, 131-142.
- Ostrowski, T. D., Sradnick, J., Stumpner, A., & Elsner, N. (2009). The elaborate courtship behavior of *Stenobothrus clavatus* Willemse, 1979 (Acrididae: Gomphocerinae). *Journal of Orthoptera Research*, 18(2), 171-182.
- Otte, D., & Williams, K. (1972). Environmentally induced color dimorphisms in grasshoppers. *Syrbula admirabilis*, *Dichromorpha viridis*, and *Chortophaga viridifasciata*. *Annals of the Entomological Society of America*, 65(5), 1154-1161(8).
- Poulton, E. B. (1890). *The colours of animals: their meaning and use, especially considered in the case of insects*. New York, New York: D. Appleton and Company.
- Rowell, C. H. F. (1971). The variable colouration of the acridoid grasshoppers. *Advances in Insect Physiology*, 8, 145-198.
- St Leger, R. J., Cooper, R. M., & Charnley, A. K. (1988). The effect of melanization of *Manduca sexta* cuticle on growth and infection by *Metarhizium anisopliae*. *Journal of Invertebrate Pathology*, 52, 459–470.
- Tsurui, K., Honma, A., & Nishida, T. (2010). Camouflage effects of various colour-marking morphs against different microhabitat backgrounds in a polymorphic pygmy grasshopper *Tetrix japonica*. *PLoS ONE*, 5(7).

- Unsicker, S. B., Köhler, G., Linz, J., Stein, C., & Weisser, W. W. (2008). Colour morph related performance in the meadow grasshopper *Chorthippus parallelus* (Orthoptera, Acrididae). *Ecological Entomology*, 33(5), 631-637.
- Wilson, K., Cotter, S. C., Reeson, A. F., & Pell, J. K. (2001). Melanism and disease resistance in insects. *Ecology Letters*, 4(6), 637-649.

Table 4.2.

Greenness values calculated for grasshoppers and their backgrounds by color-species.

Greenness can range from 0 (no green) to 1 (solid green).

Color-Species	Background	Grasshopper
Black <i>Syrbula admirabilis</i>	0.759114796	0.096857719
Green <i>Dichromorpha viridis</i>	0.52420065	0.812188149
Bicolored <i>Dichromorpha viridis</i>	0.41746981	0.199317261
Brown <i>Dichromorpha viridis</i>	0.409356419	0.012440222
Green <i>Syrbula admirabilis</i>	0.392503636	0.234378144
<i>Schistocerca americana</i>	0.388382315	0.02605857
<i>Melanoplus differentialis</i>	0.337027392	0.026232208
Brown <i>Syrbula admirabilis</i>	0.159057548	0.00721938
Brown <i>Chortophaga viridifasciata</i>	0.089792575	0.002746421
Green <i>Chortophaga viridifasciata</i>	0.087503515	0.344954622
<i>Hippiscus ocelote</i>	0.0859203	0.002360174
<i>Melanoplus femurrubrum</i>	0.081683778	0.002952408
<i>Dissosteira carolina</i>	0.058045481	0.00050752
<i>Spharagemon cristatum</i>	0.013419324	5.39445E-06

Table 4.3.

Intraspecific correlations between the greenness of the background and the time it took a user to correctly locate a grasshopper. Species that are not listed had no significant correlations.

Species with maxima listed had parabolic relationships and the maxima given is the maximum camouflage value of the parabola. The species with a slope listed had a linear relationship between background greenness and camouflage.

Color-Species	R²	Maxima	Slope
Brown <i>Dichromorpha viridis</i>	0.2871		-3.5121
<i>Dissosteira carolina</i>	0.2969	0.379583695	
Black <i>Syrbula admirabilis</i>	0.3674	0.459183673	
Green <i>Syrbula admirabilis</i>	0.4014	0.238984321	
<i>Schistocerca americana</i>	0.4382	0.314131686	
Green <i>Dichromorpha viridis</i>	0.5622	0.19299382	
<i>Hippiscus ocelote</i>	0.6258	0.576501305	
Brown <i>Chortophaga viridifasciata</i>	0.6916	0.226193527	

Table 4.4.

Residuals by color-species from a model predicting the time it took a viewer to locate a grasshopper by the greenness difference between the grasshopper and the background.

Negative residuals represent species less well-camouflaged than expected whereas positive residuals represent species that outperform the expectations of the greenness-difference model. Species are sorted in descending order by absolute value of the residual.

Color-Species	Residual
<i>Dissosteira carolina</i>	-0.83881561
<i>Schistocerca americana</i>	-0.64502358
Green <i>Chortophaga viridifasciata</i>	-0.57980367
Brown <i>Syrbula admirabilis</i>	0.47740737
<i>Hippiscus ocelote</i>	0.45636753
<i>Spharagemon cristatum</i>	0.33474069
Green <i>Dichromorpha viridis</i>	0.30931364
<i>Melanoplus differentialis</i>	0.299316
<i>Melanoplus femurrubrum</i>	0.14926661
Bicolored <i>Dichromorpha viridis</i>	0.09641017
Brown <i>Dichromorpha viridis</i>	0.08770504
Black <i>Syrbula admirabilis</i>	-0.08540404
Brown <i>Chortophaga viridifasciata</i>	-0.08301136
Green <i>Syrbula admirabilis</i>	0.02134859

CHAPTER FIVE

DOES CRYPSIS HAVE AN EVOLUTIONARY COST? AN INVESTIGATION USING PREDATOR-FREE ISLAND SPECIES

INTRODUCTION

Environmental change can render previously useful adaptations selectively neutral or reverse selection entirely. The disappearance of selectively neutral characteristics over time may take place either through replacement (the replacement of the claws of proto-ungulates by hooves) or through reduction (the loss of the hind limb bones in whales beyond what is required to streamline the animal). Because of this it is difficult to estimate the time over which a non-selective characteristic might be retained. This poses a particular problem when one seeks to draw inferences about a species' behavior and environment from its morphology, as may occur with species that are known primarily from museum specimens or for large groups in which only initial species descriptions have been published for many species (something that is frequently true of invertebrate groups). These inferences are similar to the just-so stories criticized by Gould and Lewontin (1979) and more recently Nielsen (2009) in which morphological or genetic characteristics are assigned speculative functions to explain their adaptive value in a particular environment. Janzen and Martin (1982) highlighted the danger of these inferences by proposing that, contrary to many previous ideas about Central American trees, many species may be adapted to a now-extinct guild of large herbivores and frugivores (see also Howe, 1985; Hunter, 1989; Siemens and Johnson, 1996; Guimaraes et al., 2008; Zaya and Howe, 2009).

Defensive characteristics are frequently recognizable and because predation is rarely observed in nature it is not uncommon to infer information about predator-prey interactions from adaptations that are perceived to be defensive in a prey animal. However, the existence of these traits does not always indicate anything about modern predator-prey relationships.

Byers (1997) proposed that a number of behaviors in modern pronghorn (*Antilocapra americana*) are actually adaptive only in the context of the Pleistocene predator fauna of North America, although his views have been criticized by Kitchen (1999) and Janis (1999). Diamond (1990) suggested that many plants in New Zealand are divirgating in a manner that protected them from extinct moas and Fadzly and Burns (2010) have made the same claim for the coloration of the plant *Elaeocarpus hookerianus*. Goodman (1994) discussed the possibility that modern lemur behavior is shaped in part by an extinct eagle, although this view has received criticism from Csermely (1996), and Sauther (1989) explained the behaviors under question as adaptations to the modern environment. Peckarsky and Penton (1988) noted that *Ephemerella* nymphs are not normally preyed upon by stonefly larvae but continue to exhibit an anti-predator posture when contacted by stonefly larvae. This posture primarily involves the cerci but removal of the cerci does not influence predator-induced mortality. This may indicate that the behavior is an adaptation to a previous predator-prey interaction.

Studies of the loss of various defensive characteristics within single species paint a complicated picture. Anti-predator behavior is a common characteristic to study and has been found to decrease in the absence of predators in a number of studies (Blumstein, 2002; Blumstein and Daniel, 2002; Beauchamp, 2004; Blumstein and Daniel, 2005) but not in another (van Damme and Castilla, 1996). However, even when a decrease is shown not all behaviors decrease at the same rate. Blumstein and Daniel (2005) found that the presence or absence of predators in the environment altered group size but not flight initiation distance. However, as Berger et al. (2001) demonstrated, anti-predator behavior may change in a

single individual and so loss of anti-predator behavior may not always be an evolutionary phenomenon. More convincing are cases when some anti-predator behavior is retained (Blumstein, 2002) e.g., tammar wallabies retained visual recognition of predators with which they had not been sympatric in more than a century but did not recognize the scents of these same predators. Coss (1999) reviewed the results of several previous papers on ground squirrels and their reactions to snake predators. Several components of the suite of anti-snake behaviors were retained in all populations while others were lost in squirrels that were no longer sympatric with snakes. Some squirrels used in these studies came from populations that were estimated to have last interacted with snakes 300,000-700,000 years previously.

One defensive characteristic from which inferences about predator-prey interactions are often made is camouflage. Endler (1978, 1983, 1986) found that guppies in streams without predators are much more brightly colored than guppies in streams with predators. Endler (1986) extended this observation to the related fish species *Phallocerus caudimaculatus*. Endler (1991) examined the spectral sensitivities of guppies' predators and found that guppies were most brightly patterned in colors that the predators present in a given stream could detect least well. However, in this system there was a clear selective advantage to bright colors as brightly-colored male guppies are preferred by females. Visual sexual selection is not present in all species and so it is unclear whether camouflage should be universally expected to disappear when it becomes selectively neutral.

Coloration serves three broad uses: modifying the interaction between predator and prey (crypsis, mimicry, aposematism), modifying the interaction between members of the

same species (social and sexual signaling), and thermoregulation (expanded from Endler, 1978). Other uses such as protection from ultraviolet light and structural support may also be present (Averill, 1923; Gunn, 1998; Goldstein et al., 2004). This provides some theoretical basis for expecting a general trend towards the loss of crypsis when crypsis is no longer needed. The presence of a number of de-pigmented cave animals also suggests that reduction rather than replacement can operate on the color patterns of animals.

When studying the loss of a trait such as color, which is not preserved in the fossil record, living species must be used. By comparing species that have evolved without predators against related species that have evolved with predators some conclusions can be drawn about the loss of crypsis in environments where it is selectively neutral.

Species endemic to islands offer a unique opportunity to examine the effects of predation on the evolution of species. Unlike species on the mainland, which are exposed to a complete predator fauna, species on islands are exposed to a reduced set of predators. In some cases this reduced subset of predators does not include any members capable of preying upon an endemic herbivore once it reaches adult size. By comparing species (or individuals, Blumstein and Daniel, 2005) on islands lacking predators with those on the mainland the effects of predators on the evolution of presumed defenses can be examined. Beauchamp (2004) used a similar method in which he assumed that islands harbored a reduced set of predators in his examination of the loss of flocking behavior.

I have applied the method described above to twenty-five species of mammals and birds endemic to islands that lack predators large enough to consistently take them as prey. The color patterns of these animals has been compared to that of their closest mainland

relatives living with predators and these differences have also been compared to a set of insular endemics that do suffer predation and a similar set of insular endemic predators that are expected to retain crypsis for use in stalking prey. I expect that crypsis will be lost over time as it becomes unnecessary.

METHODS

Generation of species lists

An initial list of islands was compiled by examining satellite photographs available through Google Earth and through internet searches to identify the names of islands and island groups. All islands found by whatever manner were included in the list. This list was then used as the basis for a series of searches aimed at locating insular endemic species. Only minor filtering was applied to this list. In cases in which faunal lists were found for islands with large predators, endemic taxa known to be within the appropriate prey size range for these predators were excluded. Species known to be predators themselves were recorded on a separate list. The scientific name, distribution, and larger taxonomic group were recorded for all endemic taxa. Additional searches for listed endemic species were made and taxonomic reviews were consulted to locate additional insular endemics (Nowak, 1991; Flannery 1995a, b; Monk et al., 1997; Sibley and Monroe, 1990; Sibley and Monroe, 1993; Delacour and Mayr, 1946; Holmes and Phillipps, 1996; Mayr, 1945; Sinclair and Langrand, 1998; Strange, 2000; Birdlife International, 2011).

Once the list of endemic herbivores was completed, a list of predators found on islands was created by consulting the distributional data listed for mammals (Nowak, 1991; Nowak, 2005), birds (Sibley and Monroe, 1990; Sibley and Monroe, 1993), snakes

(McDiarmid, 1999), crocodilians (Alderton, 1992), and varanoid lizards (Pianka et al., 2004). Information on taxa, whose extinction may have been anthropogenically driven, was included where it was available.

Predators were sorted into three categories: regular predators, occasional predators, and snakes. Regular predators are expected to provide constant pressure on prey species to maintain camouflage. Occasional predators are expected to provide much less pressure. Snakes, whether they prey regularly, or occasionally, on the species of interest, are expected to provide no pressure on the prey species to maintain camouflage. Snakes appear to have trouble detecting non-moving prey visually and do not appear to discriminate between realistic and non-realistic models of moving prey (Herzog and Burghardt, 1974; Drummond 1985). Additionally, the majority of snakes that could exclude an island endemic prey-species from consideration are heat-sensitive members of the genus *Python* that are capable of accurately striking prey without using visual information (Grace et al., 2001). These factors taken together suggest that predation by snakes is not influenced by the camouflage of prey.

A predatory species was considered a regular predator of a given prey-species if it was capable of following that prey-species into its normal habitat and was of sufficient size that the prey-species fell within the size range of its normal prey.

A predatory species was considered an occasional predator for one of two reasons. First, a predator might be of sufficient size to regularly take the prey-species but be incapable of following it into its normal habitat. This is the case when considering extant crocodilians as predators of terrestrial prey. Predatory encounters only occur when the prey-species

approaches a sufficiently large body of water, a different visual environment than the prey-species' normal habitat. Secondly, a predator might be able to follow the prey-species into its normal habitat but be insufficiently large to capture the prey-species as part of its normal diet. To be considered an occasional predator there must also be reason to believe that the predator occasionally took prey much larger than its usual prey items and posed a threat to the prey-species of interest on such occasions. For example, eagles routinely prey upon rabbit-sized animals but occasionally take adult ungulates.

The separation of predators into these categories was normally obvious. In two cases additional work was required. In the first, the recently-extinct possibly-terrestrial crocodilians in the genus *Mekosuchus* (Mead et al., 2002), ecological data could only be inferred. These crocodiles were treated as competent terrestrial predators for the purposes of this study. In the second case, in a variety of eagle species data on prey habits often were lacking. This is especially acute in the case of *Pithecophaga jefferyi*, a rare species of eagle reported anecdotally to prey upon small pigs and deer (Sith-Smith, 1910; Ibañez et al., 2003). This species' range no longer overlaps with that of many of the Philippine endemic species under consideration and so direct observation of predation is now impossible. Sith-Smith (1910) reported that one specimen of *P. jefferyi* was caught in a trap baited with a small pig but does not give a more exact size. Ibañez et al. (2003) observed prey being brought back to the nest of wild *P. jefferyi*. None of the prey-species observed were larger than a domestic cat despite local reports of predation upon livestock. Concepcion et al., (2009) observed a pair of *P. jefferyi* that brought three domestic dogs back to their nest although the sizes of these dogs were not noted and the majority of prey items were cloud rats and colugos.

The upper size limits of prey taken by *P. jefferyi* was estimated by comparing *P. jefferyi* to the smaller golden eagle (*Aquila chrysaetos*) and the similarly-sized martial and crowned eagles (*Polemaetus bellicosus* and *Stephanoaetus coronatus*). Two studies that examined golden eagle nests (Carnie, 1954; Molhagen et al., 1972) found ungulate remains and Cameron (1908) recorded an instance in which three golden eagles killed an adult pronghorn (*Antilocapra americana*) in deep snow. Nybakk et al., (1999) recorded three semi-domestic adult reindeer (*Rangifer tarandus*) killed by golden eagles, ranging in weight from 60-71 kg when they had last been weighed live. However, Norberg et al., (2006) estimated that the mean weight of reindeer fawns killed by golden eagles was twelve kilograms while Davis and Taylor (1939) believed that bighorn sheep (*Ovis canadensis*) became immune to eagle predation when a third to half grown. Estimates of the weight a golden eagle can carry based on prey remains (and, therefore, the prey it can most easily capture) range from eight to thirteen pounds (Cameron, 1908; Tjernberg; 1981) and Woodgerd (1952) observed a golden eagle carrying a 9.75 pound lamb for a short distance before stopping. He estimated that this lamb was at the upper range of the eagle's carrying ability.

Large martial eagles have also been recorded killing large prey including juvenile Uganda kob (*Kobus kob*) (Balmford and Turyaho, 1992) and adult steenbok (*Raphicerus campestris*) (Boshoff et al., 1990). Boshoff et al., (1990) also estimated that martial eagles killed bovids up to thirteen kilograms in mass. However, most of the prey Boshoff et al., recorded were in the 1-5 kg range and Wanzie (1986) reported that a martial eagle was observed killing, but being unable to transport, a Buffon's kob less than one week old.

Crowned eagles have been recorded killing bushbuck (*Tragelaphus scriptus*) weighing up to twenty kilograms (Brown, 1971) and a 9.1 kilogram duiker (Shultz, 2002). McGraw et al., (2006) directly addressed the issue of prey size limits stating that eagles preferred 6-10 kilogram prey and that eleven-kilogram mangabeys were carried to the nest while twenty kilogram prey were occasionally killed but had to be dismembered to be carried.

These data were used to estimate limits for both regular and occasional prey of eagles as eagles appear to be capable of killing prey much larger than their usual prey.

Creation of sets of pictures

After filtering the list of island-endemic species to remove all species that had regular predators, pictures were obtained of the remaining species when possible. Photographs were also obtained of the species' nearest relatives excluding other species that were also to be tested. For subspecies these consisted of all other subspecies in the species, for species these consisted of all other species in the genus, and for monotypic genera these consisted of all species in the most closely related genera. Because there are practical limits on how many objects humans can readily compare, several large groups of nearest relatives were reduced. When possible, phylogenetic information was used to narrow the group of relatives. When phylogenetic information was not available species were filtered by geographic range and those species whose ranges overlapped or approached the species of interest were included. Photographs were selected on the basis of good lighting, high resolution, and a clear view of the entire animal. When necessary two photographs from different angles were used.

Photographs were placed in a single large picture and each photograph or photograph cluster representing a single species or subspecies was labeled with a consecutive letter. The positions of taxa within the large picture were randomized. Five volunteers who were not familiar with the species shown examined each picture. The volunteers remained constant for the entire study. For each picture a volunteer could record that all the taxa looked different from one another, that none of the taxa looked significantly different from one another, or that one taxon looked significantly different from all others and then provided the letter of this taxon. Volunteers were instructed to use differences in color to make these distinctions.

Two additional sets of pictures were created as controls and analyzed in the same way. The first picture set tested species endemic to islands that have regular predators and the second set tested predators that are endemic to islands. Both sets were selected to maximize taxonomic and geographic overlap between the control sets and the test set. In both sets the number of monotypic genera (the only case in which comparisons were conducted across generic lines) were the same as in the test set.

Labeling of the animals' colors and patterns

Each species included in a picture set was also entered into a dataset where its colors and patterns were labeled for further analysis. Mammals were broken into ten body regions (face, head, neck, forelimbs, hind limbs, back, sides, belly, rear, and tail) and birds were broken into ten different regions (beak, head, neck, proximal and distal wing, anterior and posterior underside, back, legs, and tail). These body regions were chosen to minimize the number of doubly-labeled regions. For example, many birds had a wing that was one color

near the body and a different color near the tip. Dividing the wing into two segments allowed me to label each region with only one color rather than repeatedly labeling the entire wing with two colors. This method of determining body regions was chosen because it should produce regions which normally function as single units in the evolution of color and pattern.

Each species was compared to every other species in its picture-set and a difference-score calculated for each comparison. The sum of the difference-scores for all comparisons involving a particular species was calculated as a measure of total difference between that species and its sister taxa.

Comparisons among species were made by body region. The base colors and pattern types of each region were always compared. When the base color was the same the darkness of the color (on a scale of one to three) was compared. When the pattern was the same the pattern color was compared and when the pattern color was the same the darkness of the pattern color, the size of the pattern, and the density of the pattern were compared. Not all patterns had characteristics of size and density but where they were relevant they were both scored on a scale of one to three.

Comparisons of color could receive a difference-score of zero (no difference), one (different), or 0.5 (used to describe the difference between such pairs of colors as brown and reddish-brown, black and gray, and brown and gray). The colors black, gray, brown, reddish-brown, and green were considered to be generally cryptic while the colors white, red, orange, yellow, pink, blue, and purple were considered to be generally conspicuous. When

both colors were cryptic or conspicuous they were recorded separately from colors that were in different categories.

When a base color of a particular body region in one species was the pattern color (but not the base color) for the same body region in another species, or vice versa, the difference-score for both the base color and the pattern color was halved. If the base color and the pattern color were both present but reversed in the other species, both comparisons were divided by four.

Differences in pattern could take two forms. The first was the difference between two patterned species. In this case the difference in pattern could be zero (the same pattern on both species), one (different patterns), or 0.5 (spots on one animal and steaks or stripes on the other). In the second case one animal had more patterns on a body region than did the other animal. In this case the difference was simply the absolute value of the difference between the two pattern counts.

In all other cases the labeling took the form of a number and the difference-score was the absolute value of the difference between the numbers.

Because the final score was a sum of multiple comparisons, all involving a single species, the directionality of differences was important. In all cases when a difference could occur in one of two directions (e.g., darker or lighter) the directionality of the contrast was recorded as well as the magnitude of the contrast.

Further modification of the scores could occur in two ways. First, certain body regions were dramatically reduced in some species. In these species all the comparisons made within these body regions were divided by two. Second, some species were

polymorphic for color. The comparison-scores for each color morph were divided by the number of color morphs and then added together for the final score for the species. In cases when both species in a comparison were polymorphic for color and the number of color morphs was the same for both species the most similar color morphs were compared to one another.

Statistical analysis

The first analysis used the responses from the viewers who were asked to identify species that differed significantly from the others in the same picture set. Each picture-set received a score equal to the number of viewers who responded with the letter identifying the target taxon for that picture-set. (For the *Bubalus* species only one non-domestic species is a mainland species and so the scoring was reversed for this picture-set.) A general linear model in SAS 9.2 was used to run an F-test on the scores by group. The F-test was followed by Tukey testing to assess differences between pairs.

The remaining analyses used the difference-data from the color and pattern dataset. A general linear model assuming an underlying Poisson distribution was fitted to the data using the GENMOD procedure in SAS 9.2. The classification of a species as a bird or mammal, a predation-free endemic, a preyed-upon endemic, or a predator, and its classification as a test species or a mainland species used for comparisons were all used to predict the level of difference between the various categories of color and pattern. Combinations of classifications, such as mammalian predators, were also used.

A canonical correspondence analysis was also run using the same categories and data. Categories were numbered to allow this comparison. Binary categories were arbitrarily re-

labeled as zero and one. The three-member categories of predation-free endemic, preyed-upon endemic, or predator were labeled so that predation-free endemics were twos, preyed-upon endemics were ones, and the predators (least similar) were zeros. The canonical correspondence analysis was run using the CANCELL procedure in SAS 9.2.

Finally, the differences were compared using a sign test. Within each comparison group (picture-set) species were divided into those that had been chosen for the study (test species) and those that were included because they were related to chosen species (non-test species). The average difference score of the non-test species in a group was considered to be a baseline for that taxonomic unit. This baseline was then subtracted from the score of the test species in the group. A sign test was used to determine whether birds, mammals, predation-free endemics, preyed-upon endemics, or predators showed statistically significant deviation in score differences from zero. This analysis was run in SAS 9.2 using the UNIVARIATE procedure.

RESULTS

The study included nine species thought to be entirely free of predation. A number of potential candidates had to be excluded because they were driven into extinction by humans before adequate records of their coloration were made. One remaining group, the giant island tortoises, was excluded because tortoises derive significant protection from their shell even at small body sizes. This list of species had to be additionally shortened because no photographs could be located for four of the species (Table 5.1).

An additional sixteen species were located that appear to be predated upon only by pythons or very occasionally by large raptors taking prey well outside their normal range of prey-sizes (Table 5.1).

Preliminary testing showed no differences between subspecies within a species and so subspecies endemic to islands were not included in this analysis.

The analysis of viewer's responses found differences between the average scores of the predation-free, preyed upon, and predator groups. The average score for the predation-free group was 2.02, the average score for the preyed upon group was 0.68, and the average score for the predators was 0.55. The p-value for the F-test differentiating these groups was 0.0003. Tukey testing found significant differences between the predation-free group and both others but no difference between the control groups.

The Poisson regression found differences between groups in almost half of the categories and group classifications. Three distinct patterns emerged from the data: mammals were more likely than birds to differ in color, birds were more likely than mammals to differ in amount and type of pattern, and predators were more likely than any other group to differ in the details of their patterns.

Canonical correspondence testing found that predators were the more likely to vary than was any other group. Birds were also more variable than mammals except in the categories of darkness and lightness of base color.

Sign testing found significant differences between the difference-scores for target and non-target species only in six out of 85 cases for an analysis that separated scores based on

the direction of change, and in five out of 30 cases for an analysis that did not take direction into account.

DISCUSSION

Despite theoretical justification for my hypothesis, support for it is quite weak. The difference between the various methods of comparison is of interest but the lack of consistent support demonstrates the lack of a clear trend. The evaluation by human observers did detect the expected differences. Human observers, unlike the color-labeling system employed for the other comparisons, integrate visual information in a comprehensive manner. It is possible that the differences detected by human observers are the stacked effects of many small changes on the same visual element and that each one of these changes is too slight to be recorded in the color-labeling data. However, directionality of change was not assessed in comparisons of observer input and so my hypothesis cannot be supported using these data alone.

Since the expectation that crypsis should disappear when it is no longer selectively advantageous is in line with a number of theories about the purpose of color patterns and the retention of useless characteristics, it is worth asking why this study did not find support for this hypothesis.

First, it is possible that the predator-free islands I selected are only recently free of predators, or that the species that I believe evolved on these islands once had wider ranges that overlapped with those of predators. The recent discovery of the Vanuatu *Mekosuchus* (Mead et al., 2002) and the cautionary tale of Henderson Island's long-undiscovered human settlement and a possible anthropogenic extinction event (Steadman and Olson, 1985) serve

as reminders that the biological history of these islands may not be that inferred from current data.

Second, it is possible that a great number of the mainland animals examined are not optimized for crypsis. This is very likely in the case of some of the bird species, specifically the Psittaciformes. In these cases, crypsis is only incidental and so the loss of crypsis is essentially a random event in any taxon, without fitness cost or benefit. This could be problematic for the study of crypsis overall as relatively few species have been examined to determine whether their crypsis confers a survival advantage although it is common to assume that any animal that is hard to locate visually in its environment is gaining a survival advantage from this.

Third, it is possible that camouflage does not have a fitness cost in the absence of predators, or that it does only in some species. If cryptic colors and patterns can simultaneously serve other functions, or if those functions are not useful to the species in question, crypsis could persist without active selection for its defensive value. Forsman and Appelqvist (1998) found that black grasshoppers heated up faster than their striped conspecifics and were also harder for chickens to re-locate after the grasshopper made an escape jump. It is certainly possible that camouflage is useful for multiple purposes in the ancestral stock of some of the species examined and has been retained for its non-cryptic uses. All the species in my dataset are endotherms and so the value of coloration in altering body temperature might be expected to be low. Another major function of color, social signaling, may be unimportant due to characteristics of the particular species in question. Species with poor vision and a reliance on other senses, or species that inhabit environments

with characteristics that inhibit vision such as low light levels, may not be able to make effective use of visual signals and should not be expected to evolve them. Mammals, which rely extensively on scent, are more likely to fit this criterion than birds, which are highly visual. Since analyses were run both separately and combined for mammals and birds it remains odd that no differences were detected in the comparisons of color-labeling.

The failure to lose crypsis under conditions of little to no predation may be informative in regards to the rate of evolutionary loss of selectively-neutral characteristics. While the mechanism for this retention remains unclear, the results of this study suggest that current crypsis does not constitute proof of current visually-oriented predation. Past environments continue to influence the color patterns of current species. Researchers seeking to draw inferences about predator-prey interactions from color-patterns should be aware that there appears to be no general trend towards the loss of selectively-neutral crypsis. While in some species, such as visually-displaying poeciliid fish, the replacement of cryptic patterns by more visible ones may be expected (Endler, 1978, 1983, 1986). The life-history of a species may have a large influence on the expected rate of crypsis loss in situations in which crypsis becomes selectively-neutral. Only direct testing of crypsis in environmentally-relevant predator-prey interactions can verify that current crypsis is not an adaptation to a previous environment.

LITERATURE CITED

- Alderton, D. (1992). *Crocodiles & Alligators of the World*. Blandford: Cassell.
- Averill, C. K. (1923). Black wing tips. *Condor*, 25(2), 57-59.

- Balmford, A., & Turyaho, M. (1992). Predation risk and lek-breeding in Uganda kob. *Animal Behaviour*, 44(1), 117-127.
- Beauchamp, G. (2004). Reduced flocking by birds on islands with relaxed predation. *Proceedings of the Royal Society B?*, 271, 1039-1042.
- Berger, J., Swenson, J. E., & Persson, I.-L. (2001). Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science*, 291, 1036-1039.
- Birdlife International (2011). Endemic bird areas. Retrieved from http://www.birdlife.org/action/science/endemic_bird_areas/index.html
- Blumstein, D. T. (2002). Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *Journal of Biogeography*, 29, 685-692.
- Blumstein, D. T., & Daniel, J. C. (2002). Isolation from mammalian predators differentially affects two congeners. *Behavioral Ecology*, 13, 657-663.
- Blumstein, D. T., & Daniel, J. C. (2005). The loss of anti-predator behaviour following isolation on islands. *Proceedings: Biological Sciences*, 272(1573), 1663-1668.
- Boshoff, A. F., Palmer, N. G., & Avery, G. (1990). Regional variation in the diet of martial eagles in the Cape Province, South Africa. *South African Journal of Wildlife Research*, 20(2), 57-68.
- Brown, L. H. (1971). The relations of the crowned eagle *Stephanoaetus coronatus* and some of its prey animals. *Ibis*, 113(2), 240-243.
- Byers, J. A. (1997). *American pronghorn: Social adaptations and the ghosts of predators past*. Chicago: University Chicago Press.
- Cameron, E. S. (1908). Observations on the golden eagle in Montana. *The Auk*, 25(3), 251-268.
- Carnie, S. K. (1954). Food habits of nesting golden eagles in the coast ranges of California. *The Condor*, 56(1), 3-12.
- Concepcion, C., Sulapas, M., & Ibañez, J. (2009). Notes on food habits and breeding and nestling behavior of Philippine eagles in Mt. Apo Natural Park, Mindanao Islands, Philippines. *Banwa: Natural Sciences*, 3(1&2).
- Coss, R. G. (1999). Effects of relaxed natural selection on the evolution of behavior. In S. A. Foster & J A Endler (Eds.), *Geographic variation in behavior: perspectives on evolutionary mechanisms* (pp. 180-20). Oxford: Oxford University Press.

- Csermely, D. (1996). Antipredator behavior in lemurs: Evidence of an extinct eagle on Madagascar or something else? *International Journal of Primatology*, 17(3), 349-354.
- van Damme, R., & Castilla, A. M. (1996). Chemosensory predator recognition in the lizard *Podarcis hispanica*: effects of predation pressure relaxation. *Journal of Chemical Ecology*, 22, 13-22.
- Davis, W. B., & Taylor, W. P. (1939). The bighorn sheep of Texas. *Journal of Mammalogy*, 20(4), 440-455.
- Delacour, J., & Mayr, Ernst. (1946). *Birds of the Philippines*. New York: Macmillan.
- Diamond, J. M. (1990). Biological effects of ghosts. *Nature*, 345, 769-770.
- Drummond, H. (1985). The role of vision in the predatory behaviour of natricine snakes. *Animal Behaviour*, 33(1), 206-215.
- Endler, J.A. (1983). Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, 9, 173-190.
- Endler, John A. (1978). A predator's view of animal color patterns. *Evolutionary Biology*, 11, 319-364.
- Endler, John A. (1986). Convergent and divergent effects of natural selection on color patterns in two fish faunas. *Evolution*, 36, 178-188.
- Endler, John A. (1991). Variation in the appearance of guppy color patterns to guppies and their predators under different visual conditions. *Vision Research*, 31, 587-608.
- Fadzly, N., & Burns, K. C. (2010). Hiding from the ghost of herbivory past: Evidence for crypsis in an insular tree species. *International Journal of Plant Sciences*, 171(8), 828-833.
- Flannery, T. (1995). *Mammals of New Guinea*. Reed Books and Cornell University Press.
- Flannery, T. (1995). *Mammals of the South-West Pacific & Moluccan Islands*. Reed Books and Cornell University Press.
- Forsman, A., & Appelqvist, S. (1998). Visual predators impose correlational selection on prey color pattern and behavior. *Behavioral Ecology*, 9(4), 409-413.
- Goldstein, G., Flory, K. R., Browne, B. A., Majid, S., Ichida, J. M., & Burt Jr., E. H. (2004). Bacterial degradation of black and white feathers. *The Auk*, 121(3), 656-659.

- Goodman, S. M. (1994). The enigma of antipredator behavior in lemurs: Evidence of a large extinct eagle on Madagascar. *International Journal of Primatology*, 15(1), 129-134.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B*, 205(581-598).
- Grace, M. S., Woodward, O. M., Church, D. R., & Calisch, G. (2001). Prey targeting by the infrared-imaging snake *Python molarus*: effects of experimental and congenital visual deprivation. *Behavioural Brain Research*, 119(1), 23-31.
- Guimaraes, P. R., Galetti, M., & Jordano, P. (2008). Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. *PLoS ONE*, 3(3), Article Number: e1745.
- Gunn, A. (1998). The determination of larval phase coloration in the African armyworm, *Spodoptera exempta* and its consequences for thermoregulation and protection from UV light. *Entomologia Expis Applicata*, 86, 125–133.
- Herzog Jr., H. A., & Burghardt, G. M. (1974). Prey movement and predatory behavior of juvenile Western yellow-bellied racers, *Coluber constrictor mormon*. *Herpetologica*, 30(3), 285-289.
- Holmes, D., & Phillipps, K. (1996). *The Birds of Sulawesi*. Oxford University Press.
- Howe, Henry F. (1985). Gomphothere fruits: A critique. *The American Naturalist*, 125(6), 853-865.
- Hunter, J. R. (1989). Seed dispersal and germination of *Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae: Mimosoideae): Are megafauna necessary? *Journal of Biogeography*, 16, 369–378.
- Ibañez, J. C., Jr., H. C. M., Balaquit-Ibañez, G., Afan, D. S., & Kennedy, R. S. (2003). Notes on the breeding behavior of a Philippine eagle pair at Mount Sinaka, Central Mindanao. *The Wilson Bulletin*, 115(3), 333-336.
- Janis, C. (1999). Reviewed work(s): American Pronghorn: Social Adaptations and the Ghosts of Predators Past by John A. Byers. *The Quarterly Review of Biology*, 74(1), 108-109.
- Janzen, D. H., & Martin, P. S. (1982). Neotropical anachronisms: The fruits the gomphotheres ate. *Science, New Series*, 215(4528), 19-27.
- Kitchen, D. W. (1999). Review: Ghosts of predators past or dancing with wolves? Reviewed work(s): American Pronghorn: Social Adaptations and the Ghost of Predators Past by J. A. Byers. *Global Ecology and Biogeography*, 8(¾), 318-319.

- Mayr, E. (1945). *Birds of the Southwest Pacific: A Field Guide to the Birds of the Area Between Samoa, New Caledonia, and Micronesia*. New York: The MacMillan Company.
- McDiarmid, R. W., Campbell, J. A., & Toure, T. A. (1999). *Species of the World: A Taxonomic and Geographic Reference Volume 1*. The Herpetologists' League.
- McGraw, W. S., Cooke, C., & Shultz, S. (2006). Primate remains from African crowned eagle (*Stephanoaetus coronatus*) nests in Ivory Coast's Tai Forest: Implications for primate predation and early hominid taphonomy in South Africa. *American Journal of Physical Anthropology*, 131(2), 151–165.
- Mead, J. I., Steadman, D. W., Bedford, S. H., Bell, C. J., & Spriggs, M. (2002). New extinct mekosuchine crocodile from Vanuatu, South Pacific. *Copeia*, (3), 632-641.
- Mollhagen, T. R., Wiley, R. W., & Packard, R. L. (1972). Prey remains in golden eagle nests: Texas and New Mexico. *The Journal of Wildlife Management*, 36(3), 784-792.
- Monk, K. A., De Fretes, Y., & Lilley, G. R. (1997). *The Ecology of Nusa Tenggara and Maluku*. Periplus Editions (HK) Ltd.
- Nielsen, R. (2009). Adaptionism-30 years after Gould and Lewontin. *Evolution*, 63(10), 2487-2490.
- Norberg, H., Kojola, I., Aikio, P., & Nylund, M. (2006). Predation by golden eagle *Aquila chrysaetos* on semi-domesticated reindeer *Rangifer tarandus* calves in northeastern Finnish Lapland. *Wildlife Biology*, 12(4), 393-402.
- Nowak, R. M. (1991). *Walker's Mammals of the World, Fifth Edition Volume II*. Baltimore and London: The Johns Hopkins University Press.
- Nowak, R. M. (1995). *Walker's Carnivores of the World. 1995*. Baltimore and London: The Johns Hopkins University Press.
- Nowak, R. M. (2005.). *Walker's Mammals of the World, Fifth Edition Volume I*. Baltimore and London: The Johns Hopkins University Press.
- Nybakk, K., Kjølsvik, O., & Kvam, T. (1999). Golden eagle predation on semidomestic reindeer. *Wildlife Society Bulletin*, 27(4), 1038-1042.
- Peckarsky, B. L., & Penton, M. A. (1998). Why do *Ephemerella* nymphs scorpion posture: a “ghost of predation past”? *Oikos*, 53, 185–193.

- Pianka, E. R., King, D. R., & King, R. A. (2004). *Varanoid Lizards of the World*. Bloomington & Indianapolis: Indiana University Press.
- Sauther, M. L. (1989). Antipredator behavior in troops of free-ranging *Lemur catta* at Beza Mahafaly special reserve. *Madagascar*, 10(6), 595-606.
- Shultz, S. (2002). Population density, breeding chronology and diet of Crowned Eagles *Stephanoaetus coronatus* in Tai National Park, Ivory Coast. *Ibis*, 144(1), 135–138.
- Sibley, C. G., & Monroe Jr, B. L. (1990). *Distribution and Taxonomy of Birds of the World*. New Haven and London: Yale University Press.
- Sibley, C. G., & Monroe Jr, B. L. (1993). *A Supplement to Distribution and Taxonomy of Birds of the World*. New Haven and London: Yale University Press.
- Siemens, D. H., & Johnson, C. D. (1996). Bruchid oviposition patterns beneath guanacaste trees (Mimosaceae) in Venezuela: Probable consequences of extinct seed dispersers. *Biotropica*, 28(1), 96-104.
- Sinclair, I., & Langrand, O. (1998). *Birds of the Indian Ocean Islands: Madagascar, Mauritius, Reunion, Rodrigues, Seychelles and the Comoros*. Struik Publishers (Pty) Ltd.
- Sith-Smith, D. (1910). On the monkey-eating eagle of the Philippines. *Ibis*, 52(2), 285–290.
- Steadman, D. W., & Olson, S. L. (1985). Bird remains from an archaeological site on Henderson Island, South Pacific: Man-caused extinctions on an “uninhabited” island. *Proceedings of the National Academy of Sciences of the United States of America*, 82(18), 6191-6195.
- Strange, M. (2000). *A Photographic Guide to the Birds of Southeast Asia Including the Philippines & Borneo*. Periplus Editions (HK) Ltd.
- Tjernberg, M. (1981). Diet of the golden eagle *Aquila chrysaetos* during the breeding season in Sweden. *Holarctic Ecology*, 4(1), 12-19.
- Wanzie, C. (1986). Mortality factors of Buffon’s kob *Kobus kob kob* (Erxleben) in Waza National Park, Cameroon. *Mammalia*, 50(3), 351–356.
- Woodgerd, W. (1952). Food habits of the golden eagle. *The Journal of Wildlife Management*, 16(4), 457-459.
- Zaya, D. N., & Howe, H F. (2009). The anomalous Kentucky coffeetree: megafaunal fruit sinking to extinction? *Oecologia*, 161(2), 221-226.

Table 5.1. Species included in this study.

Species Name	Compared to:	
Predator-free insular endemics		
<i>Bubalus depressicornis</i>	<i>Bubalus arnee</i>	
<i>Bubalus mindorensis</i>	<i>Bubalus arnee</i>	
<i>Ptilinopus insularis</i>	<i>Ptilinopus porphyraceus</i>	<i>Ptilinopus rarotongensis</i>
	<i>Ptilinopus purpuratus</i>	<i>Ptilinopus chalcurus</i>
	<i>Ptilinopus coralensis</i>	<i>Ptilinopus huttoni</i>
	<i>Ptilinopus dupetithouarsii</i>	
<i>Vini kuhlii</i>	<i>Vini australis</i>	<i>Vini peruviana</i>
	<i>Vini ultramarina</i>	
<i>Vini stepheni</i>	<i>Vini australis</i>	<i>Vini peruviana</i>
	<i>Vini ultramarina</i>	
Snakes as only predators		
<i>Hylobates klossi</i>	<i>Hylobates lar</i>	<i>Hylobates agilis</i>
	<i>Hylobates muelleri</i>	<i>Hylobates moloch</i>
	<i>Hylobates pileatus</i>	
<i>Presbytis potenziani</i>	<i>Presbytis femoralis</i>	<i>Presbytis melalophos</i>
	<i>Presbytis thomasi</i>	
<i>Nasalis concolor</i>	<i>Nasalis larvatus</i>	
<i>Macaca pagensis</i>	<i>Macaca nemestrina</i>	<i>Macaca tonkeana</i>
	<i>Macaca maura</i>	<i>Macaca ochreata</i>
	<i>Macaca nigra</i>	
<i>Macaca siberu</i>	<i>Macaca nemestrina</i>	<i>Macaca tonkeana</i>
	<i>Macaca maura</i>	<i>Macaca ochreata</i>
	<i>Macaca nigra</i>	
<i>Babyrousa celebensis</i>	<i>Potamochoerus porcus</i>	<i>Potamochoerus larvatus</i>
	<i>Hylochoerus meinertzhageni</i>	
<i>Rusa alfredi</i>	<i>Rusa timorensis</i>	<i>Rusa unicolor</i>
<i>Rusa mariannus</i>	<i>Rusa timorensis</i>	<i>Rusa unicolor</i>
<i>Hystrix pumila</i>	<i>Hystrix crassispinis</i>	<i>Hystrix sumatrae</i>
<i>Pentalagus furnessi</i>	<i>Romerolagus diazi</i>	<i>Bunolagus monticularis</i>
	<i>Oryctolagus cuniculus</i>	<i>Caprolagus hispidus</i>
<i>Sus ahenobarbus</i>	<i>Sus scrofa</i>	<i>Sus verrucosus</i>
	<i>Sus barbatus</i>	
<i>Sus cebifrons</i>	<i>Sus scrofa</i>	<i>Sus verrucosus</i>
	<i>Sus barbatus</i>	

Table 5.1 continued

<i>Sus celebensis</i>	<i>Sus scrofa</i>	<i>Sus verrucosus</i>
	<i>Sus barbatus</i>	
<i>Sus philippensis</i>	<i>Sus scrofa</i>	<i>Sus verrucosus</i>
	<i>Sus barbatus</i>	
<i>Axis kuhlii</i>	<i>Axis axis</i>	<i>Axis porcinus</i>
<i>Axis calamianensis</i>	<i>Axis axis</i>	<i>Axis porcinus</i>
Insular endemics with predators		
<i>Cacatua haematurophygia</i>	<i>Cacatua sanguinea</i>	<i>Cacatua pastinator</i>
	<i>Cacatua tenuirostris</i>	
<i>Nesolagus netscheri</i>	<i>Nesolagus timminsi</i>	
<i>Macaca cyclopis</i>	<i>Macaca fascicularis</i>	<i>Macaca mulatta</i>
<i>Macaca fuscata</i>	<i>Macaca fascicularis</i>	<i>Macaca mulatta</i>
<i>Meropogon forsteni</i>	<i>Merops brewerii</i>	<i>Merops muelleri</i>
	<i>Merops gularis</i>	
<i>Muntiacus atherodes</i>	<i>Muntiacus muntjak</i>	<i>Muntiacus feae</i>
	<i>Muntiacus vuquangensis</i>	
<i>Aepyodius bruijnii</i>	<i>Alectura lathamii</i>	<i>Megapodius reinwardt</i>
	<i>Macrocephalon maleo</i>	<i>Leipoa ocellata</i>
<i>Platycercus caledonicus</i>	<i>Platycercus elegans</i>	<i>Platycercus venustus</i>
	<i>Platycercus adscitus</i>	<i>Platycercus eximius</i>
	<i>Platycercus icterotis</i>	
<i>Macaca tonkeana</i>	<i>Macaca silenus</i>	<i>Macaca nemestrina</i>
	<i>Macaca sylvanus</i>	
<i>Presbytis comata</i>	<i>Presbytis femoralis</i>	<i>Presbytis siamensis</i>
	<i>Presbytis frontata</i>	<i>Presbytis hosei</i>
<i>Presbytis melalophos</i>	<i>Presbytis femoralis</i>	<i>Presbytis siamensis</i>
	<i>Presbytis frontata</i>	<i>Presbytis hosei</i>
<i>Procolobus kirkii</i>	<i>Procolobus tephrosceles</i>	<i>Procolobus gordonorum</i>
	<i>Procolobus rufomitratus</i>	
<i>Rusa timorensis</i>	<i>Rusa unicolor</i>	
<i>Trachypithecus vetulus</i>	<i>Trachypithecus johnii</i>	
<i>Capricornis swinhoei</i>	<i>Capricornis sumatraensis</i>	<i>Capricornis milneedwardsii</i>
	<i>Capricornis rubidus</i>	<i>Capricornis thar</i>
<i>Hystrix javanica</i>	<i>Hystrix brachyura</i>	<i>Hystrix indica</i>
<i>Macaca nigra</i>	<i>Macaca silenus</i>	<i>Macaca nemestrina</i>
	<i>Macaca sylvanus</i>	
<i>Thylogale browni</i>	<i>Thylogale stigmatica</i>	<i>Thylogale thetis</i>
<i>Hylobates muelleri</i>	<i>Hylobates lar</i>	<i>Hylobates agilis</i>
	<i>Hylobates pileatus</i>	

Table 5.1 continued

<i>Hylobates moloch</i>	<i>Hylobates lar</i>	<i>Hylobates agilis</i>
	<i>Hylobates pileatus</i>	
<i>Macaca ochreata</i>	<i>Macaca silenus</i>	<i>Macaca nemestrina</i>
	<i>Macaca sylvanus</i>	
<i>Moschiola meminna</i>	<i>Moschiola indica</i>	
Insular endemic predators		
<i>Nisaetus lanceolatus</i>	<i>Nisaetus cirrhatus</i>	<i>Nisaetus nipalensis</i>
	<i>Nisaetus alboniger</i>	<i>Nisaetus nanus</i>
<i>Neofelis diardi</i>	<i>Neofelis nebulosa</i>	
<i>Meles anakuma</i>	<i>Meles leucurus</i>	<i>Meles meles</i>
<i>Melogale orientalis</i>	<i>Melogale moschata</i>	<i>Melogale personata</i>
<i>Macrogalidia musschenbroekii</i>	<i>Paguma larvata</i>	<i>Paradoxurus hermaphroditus</i>
	<i>Paradoxurus jerdoni</i>	
<i>Dasyurus albopunctatus</i>	<i>Dasyurus geoffroii</i>	<i>Dasyurus hallucatus</i>
	<i>Dasyurus maculatus</i>	<i>Dasyurus viverrinus</i>
<i>Ninox natalis</i>	<i>Ninox rufa</i>	<i>Ninox strenua</i>
	<i>Ninox connivens</i>	<i>Ninox novaeseelandiae</i>
<i>Otus mentawi</i>	<i>Otus sagittatus</i>	<i>Otus rufescens</i>
	<i>Otus lettia</i>	<i>Otus bakkamoena</i>
	<i>Otus spilocephalus</i>	<i>Otus sunia</i>
<i>Paradoxurus lignicolor</i>	<i>Paradoxurus hermaphroditus</i>	<i>Paradoxurus jerdoni</i>
<i>Pithecophaga jefferyi</i>	<i>Circaetus gallicus</i>	<i>Spilornis cheela</i>
<i>Prionailurus iriomotensis</i>	<i>Prionailurus bengalensis</i>	<i>Prionailurus planiceps</i>
	<i>Prionailurus rubiginosus</i>	<i>Prionailurus viverrinus</i>
<i>Procyon pygmaeus</i>	<i>Procyon lotor</i>	<i>Procyon cancrivorus</i>
<i>Profelis badia</i>	<i>Profelis temminckii</i>	
<i>Spizaetus bartelsi</i>	<i>Nisaetus cirrhatus</i>	<i>Nisaetus nipalensis</i>
	<i>Nisaetus alboniger</i>	<i>Nisaetus nanus</i>
<i>Urocyon littoralis</i>	<i>Urocyon cinereoargenteus</i>	
<i>Paradoxurus zeylonensis</i>	<i>Paradoxurus hermaphroditus</i>	<i>Paradoxurus jerdoni</i>
<i>Nasua nelsoni</i>	<i>Nasua narica</i>	<i>Nasua nasua</i>
<i>Mustela itatsi</i>	<i>Mustela altaica</i>	<i>Mustela erminea</i>
	<i>Mustela eversmanii</i>	<i>Mustela nivalis</i>
	<i>Mustela sibirica</i>	
<i>Haliaeetus sanfordi</i>	<i>Haliaeetus leucogaster</i>	<i>Haliaeetus leucoryphus</i>
	<i>Haliaeetus albicilla</i>	<i>Haliaeetus pelagicus</i>
<i>Buteo galapagoensis</i>	<i>Buteo swainsoni</i>	<i>Buteo brachyurus</i>
<i>Aviceda madagascariensis</i>	<i>Aviceda cuculoides</i>	<i>Aviceda jerdoni</i>
	<i>Aviceda leuphotes</i>	<i>Aviceda subcristata</i>

Table 5.1 continued

<i>Circus maillardi</i>	<i>Circus aeruginosus</i>	<i>Circus maurus</i>
	<i>Circus pygargus</i>	<i>Circus ranivorus</i>
	<i>Circus spilonotus</i>	

CHAPTER SIX
CONCLUSIONS

INTRODUCTION

Almost all species of animals defend themselves in more than one way. The manner in which these defenses relate to one another may vary widely. Dewitt et al. (1999) suggested four categories of relationships between defensive traits. Traits that are linked mechanically (such as flight and wings) are considered codependent. Traits that are effective together but ineffective separately (such as a crypsis and freezing behavior) are complementary. Finally, traits that can be used separately (such as a powerful bite and rapid escape) but are positively correlated are cospecialized whereas traits that are negatively correlated are compensatory. Cospecialization can only occur in environments where relatively undefended individuals do not suffer prohibitively high mortality. Compensation is more likely to occur in environments in which defensive traits are both necessary and extremely costly, preventing any individual from supporting more than one strongly-expressed defense.

The issue of the relationships of traits has been widely reviewed in the literature on escape behavior. Flight initiation distance has been shown to vary in response to habitat (Gutzwiller and Marcum, 1997; Fernandez-Juricic et al., 2002; Amo et al., 2007; Goodman, 2009), temperature (in ectotherms) (Rand, 1964; Hertz et al., 1982), body size (Forsman and Appelqvist, 1998; Blumstein et al., 2005; de Barros et al., 2010), predator species (Walther, 1969), visibility (Cuadrado et al., 2001), and coloration (Heatwole, 1968; Carretero et al., 2006; Cabido et al., 2009).

The relationship between escape behavior and camouflage appears to be compensatory with fleeing animals being easier to see when predators are further away.

Since flight and crypsis are mutually exclusive at any given moment (Broom & Ruxton, 2005), this result makes intuitive sense. However, the best theoretical explanation of this relationship requires that camouflage has costs that promote its absence when and where it is not necessary. While there are good reasons to believe that camouflage has costs (Ruxton et al., 2005), evidence of these costs has been demonstrated only for specific species (e.g., Forsman, 1997 and Endler, 1978). The evidence in chapter four of this present document suggests that in other species there may not be any cost to maintaining camouflage when it is not needed. In these cases the relationship between camouflage and escape is expected to be less clear as there will be no pressure to lose camouflage if a species switches to a flight-based primary defense.

The relationship between escape behavior and habitat or habitat choice is much less clear and appears to vary by species. One difficulty in determining a single theoretical model linking camouflage and habitat is that habitat alters the visibility of the prey, the visibility of the predators, and often the number and species of predators as well. If habitat influenced only the visibility of the prey, less-visible prey would be expected to show less extreme escape behavior, much as is seen with camouflage. However, the addition of variable threat confuses this issue.

Despite studies that have examined the links between escape behavior and habitat or camouflage, no studies appear to have examined all three variables simultaneously and most of the work on escape behavior has been carried out on vertebrates. Given that habitat choice can significantly alter the visibility of even an uncamouflaged animal and that rapid escape interferes with camouflage, there is an expectation that these three variables will be

correlated with one another. The data from grasshoppers that have been reported in the previous chapters provides an opportunity to examine all three of these variables together in a group of invertebrate species.

As described above, I expect that escape behavior and camouflage will be related in a compensatory manner. Furthermore, I believe that escape behavior and habitat preference will be related in the same manner because longer flight times (and shorter flight initiation distances) are most useful in avoiding attack by larger predators which are less well-concealed by obscuring vegetation. This approximates a situation in which the grasshoppers gain camouflage through habitat selection.

METHODS

Statistical Analysis

Data were drawn from the previous three studies on habitat preference, escape behavior, and camouflage. R 2.13.1 was used for all analyses. Four models were constructed: a habitat-camouflage model, a habitat-escape behavior model, an escape behavior-camouflage model, and a model integrating all three areas of research. For each model the stepAIC command was used to provide suggested best-fit models using the AIC criterion. The glm command was used to model various possibilities. Several models were also tested using datasets without *Schistocerca americana* which had an extreme value in several categories. In some cases the presence of *Schistocerca* was found to determine the form of the model and new models were created for the reduced dataset.

Phylogenetic Analysis

The phylogenetic analysis described in Chapter 3 of the present work was extended to habitat-preference variables. In summary, this method calculated the differences in a quantitative variable for a given species and its nearest relatives. The sum of these differences calculated for all species is expected to be shorter the more closely the variable of interest is correlated to phylogeny.

To analyze a variable a Monte Carlo simulation was run in R in which the values for each of the nine species was randomly reassigned on the phylogenetic tree 100,000 times and the sum of the nearest-neighbor differences calculated each time. The histogram of sums generated in this fashion defines a probability distribution for the sum of nearest-neighbor differences under the condition that phylogeny is entirely uncorrelated with the variable of interest.

RESULTS

Camouflage and escape behavior

None of the camouflage variables was found to have a significant correlation to any of the escape behavior variables.

Camouflage and habitat preference

None of the direct measures of camouflage variables was found to have a significant correlation with any of the habitat-preference variables. However, camouflage is strongly correlated with the difference between the greenness of the grasshopper and the greenness of the background. This difference (hereafter referred to as the greenness difference) was correlated with habitat preference.

Two measures of habitat preference were available: (1) the preference for short vegetation versus tall vegetation and (2) the preference for bare ground versus vegetated cover (hereafter referred to as bare-ground preference). Bare-ground preference was significantly correlated with the greenness difference with a p-value of 0.021 and an R^2 of 0.3702. Color-species (any group that differed from other groups either by species or by color morph) that preferred bare ground more strongly had lower greenness differences.

When color-species were separated into green and brown groups the correlation was shown to be primarily a product of the brown color-species. The green color-species showed no correlation between bare ground preference and greenness difference and the brown color-species showed the same correlation as the entire group ($p = 0.04484$) and the R^2 remained nearly identical (0.3821).

Escape behavior and habitat preference

Flight initiation distance (FID) is correlated with bare-ground preference. This correlation is marginally significant ($p = 0.0945$) in a model including all species. However, the removal of *Schistocerca americana*, which had the highest FID paired with a very low bare-ground preference, in opposition to the general trend, caused the p-value to become highly significant (0.00095). The R^2 for this model was 0.8341.

With *Schistocerca* removed from the dataset the correlation between flight distance and bare-ground preference was also significant ($p = 0.0026$, $R^2 = 0.7700$). This is to be expected as FID and flight distance are highly correlated.

Escape behavior, habitat preference, and camouflage

The best model relating all three categories of variables together is a model that predicted the preference for bare ground by FID, body length (head to wingtips), and their interaction term. Both FID and the FID-length interaction are significant with $p < 0.001$ under both the species and color-species grouping schemes. However, as *Schistocerca americana* had been shown to drive the relationships in other models and since *Schistocerca* is the longest species in the study by a considerable margin, a best model for the dataset without *Schistocerca* was also found. In this model, again grouping by species and by color-species, bare-ground preference is predicted by the camouflage score, body length, and FID and all two-way interactions between these variables. In the model using species' averages, the FID and FID-length interactions are significant ($p = 0.0460$ and 0.0362 , respectively) and the camouflage score is marginally significant with a p-value of 0.0833 . In the model using color-species averages, the significance of the terms is not altered but the p-values are 0.00987 (FID), 0.00318 (FID-length interaction), and 0.09186 (camouflage). Notably, while the interaction terms for camouflage were not significant, removing them from the model caused the AIC to rise significantly.

Phylogeny

The sum of nearest-neighbor distances for FID was shorter than 90.6% of the distances generated in the Monte Carlo simulation. Flight distance showed a similar pattern with the true value being shorter than 93.6% of the Monte Carlo distances. Neither habitat variable appeared to be well correlated with phylogeny. For the short-vegetation/tall-vegetation preference the true value was below only 48.6% of the Monte Carlo distribution.

The bare-ground/vegetative-cover preference had a true value below only 23.6% of the Monte Carlo distribution. Camouflage scores were also not well correlated with phylogeny, with only 3.0% of the Monte Carlo distribution below the true value. Body length was strongly correlated with phylogeny. Nearly 97% of the Monte Carlo distribution was lower than the true value.

DISCUSSION

Overall, habitat preferences were closely correlated with escape behavior while camouflage was either not correlated with either of the other factors or was correlated with them very poorly.

The correlation between habitat choice and escape behavior appears to be compensatory. Species that preferred more heavily vegetated habitats had shorter FIDs and flight distances. All else being equal, these species would spend less time and energy actively escaping. The costs of escaping in this situation extend beyond the direct costs of flight. One of the more important invertebrate predators of grasshoppers are robber flies (Asilidae) (Joern and Rudd, 1982) which primarily attack airborne prey. Notably, *Dichromorpha viridis* reduces this threat as most individuals are brachypterous. *D. viridis* is also the species with the highest preference for vegetated cover. Some flightier species may also avoid robber-fly predation through size (although this does not mean that the threat of robber flies caused these species to evolve large size). Most of the species with long FIDs are also significantly larger than the most common species of robber fly observed on the study sites. While robber flies were observed taking very large prey these observations were

infrequent and I believe that for the larger species of grasshopper robber flies are probably limited to taking only the smaller individuals.

It is also possible that the benefits of vegetative cover are lost to an actively escaping animal. Certainly, flying animals are much more visible than the same animal in the vegetation. However, many species with shorter escape distances frequently escaped by hopping not flying. Hopping animals are certainly more visible than still ones but animals hopping in tall vegetation may be lost as they re-enter the vegetation. It is possible that *Dichromorpha viridis*'s wing reduction is actually an adaptation allowing it to more easily push its way into thicker vegetation as it escapes rather than exposing itself through aerial motion.

The presence of differing escape strategies under different vegetative conditions brings up the possibility that the correlation between habitat and escape behavior is not a trade-off between avoiding detection (by being visual obscured) and evading capture, but is actually the reflection of two different strategies for evading capture. While this theory is bolstered by the differences in predator regimes between vegetated and bare habitats (invertebrate predators are expected to become more common in vegetated habitat [McNett and Rypstra, 2000; Langellotto and Denno, 2004]), I do not believe that the theory is correct. If there exist two strategies for evading capture, one in which a predator is out-flown and one in which the prey item moves a short distance and hides itself, one would expect a bimodal distribution of escape distances. Animals that were relying on hiding themselves would move a short distance and hide while animals that were relying on out-flying predators would move a long distance. Only rarely would moving an intermediate distance make sense. If

cover were available nearby, this would simply add cost to the hiding strategy while not achieving the goals of the out-flying strategy. However, no evidence of a bimodal distribution of escape distances was found for any species or for the entire group of species.

The only correlation found between camouflage and habitat choice was that the difference in greenness between the background and the grasshopper, which explained most of the variation in camouflage, was correlated with preference for vegetative cover. This trend in differences in greenness was present only in predominantly brown species. The analysis of background colors in the photographs of grasshoppers suggests that there are more completely brown environments than there are completely green ones. It may be that whereas green grasshoppers are always in environments of mixed color, some brown grasshoppers on completely bare ground are in entirely brown environments. However, splitting the population into green and brown species-groups lowers the sample size significantly and it is possible that the trend is driven by only one or two species. The lack of a discernable trend relating more direct measures of camouflage to habitat further threatens the validity of the relationship between greenness differences and habitat. Further investigation would be needed to determine the validity of this correlation.

Because the three-factor models (those that included escape behavior, camouflage, and habitat choice) with and without *Schistocerca americana* differed by much as they did, it seems reasonable to suggest that *S. americana* is a true outlier. Unlike all other species studied, *S. americana* overwinters as an adult which means that the adults of *S. americana* must survive much longer than other species and must do so under conditions in which they are one of the few insect species available to predators (Kuitert and Connin, 1952). The price

S. americana pay for this survival is presumably that of greatly increased defenses (although, as a very large species, *S. americana* probably does not suffer additional flight costs from robber-fly predation).

The model without *S. americana* should then represent the relationships between escape behavior, camouflage, and habitat preference in a group of species with a more comparable level of predatory threat. In this model the strong correlation between preference for bare ground and a long FID (or flight distance, since these are also correlated) is preserved. The interaction between FID and body length is also significant, although body length itself is not. This, however, may be driven by a single species with an unusually high residual in the FID-bare ground preference model, which also has the longest body length once *S. americana* is removed. The marginal significance of camouflage is more interesting as this is the first model in which camouflage has played any role. There is a very slight trend towards higher levels of camouflage with a higher preference for bare ground and a longer FID. This is contrary to my expectation that camouflage and active escape would act in a compensatory manner because active escape nullifies the usefulness of camouflage. However, it may be that camouflage and active escape act in a cospecialized manner in which both defenses together allow a species to occupy a niche that would otherwise be too dangerous, much as I have proposed that escape behavior and habitat choice act as cospecialized defenses that allow *S. americana* to occupy a dangerous temporal habitat.

Notably, the relationships between all three factors seem to be driven by the costs associated with particular forms of defense. Habitat preference is only partly a defense but the costs associated with confining oneself to a particular habitat are clear. The costs of

active escape, both in direct costs and in terms of potential robber-fly predation, are also rather high. These two defenses are correlated in clearly discernable ways. Camouflage, which is not clearly related to anything else, may have much lower costs. The costs associated with camouflage are primarily opportunity costs but it is not clear exactly how beneficial the opportunities that are being missed might be to the grasshopper. The analysis described in the fourth chapter suggests that camouflage may be a low-cost defense and that it may not be replaced by other patterns when it is no longer needed. If this is true then over the course of evolutionary time escape behavior and habitat choice may change more rapidly while camouflage is only slowly replaced. This would explain the low strength of the relationship between camouflage and the potentially higher-cost defenses that was seen in this study.

One of the most interesting findings of this study is that while measures of escape behavior are related to measures of camouflage and habitat preference, only escape behavior is strongly related to phylogeny. While behavior is normally thought of as a highly malleable trait in this study it appears that behavior may have been more static over evolutionary time, with grasshoppers evolving other defenses (camouflage and defensive habitat preferences) that compensate for any shortfalls in escape behavior. This conservatism is especially odd when the differing flight capacities of some of the closely-related species are considered. For instance, *Syrbula admirabilis* and *Dichromorpha viridis* are each other's closest relatives in this study and both have similar FID and flight distances. However, *S. admirabilis* is capable of flight, including occasional sustained flights, while most individual *D. viridis*, including

all individuals observed during this study, are not. The evolutionary conservatism of some unexpected traits clearly requires further investigation.

Other interesting lines of further research include a more thorough examination of the benefits *Schistocerca americana* gains by overwintering as an adult. Since it appears to pay a substantial price for this behavior, the rewards should be equally great but are, as yet, unknown. Theoretical work that examines the relationship between camouflage and visual obstructions might also explain some of the more confusing aspects of the relationship (or non-relationship) between camouflage and habitat preference.

LITERATURE CITED

- Amo, L., Lopez, P., & Martin, J. (2007). Habitat deterioration affects antipredatory behavior, body condition, and parasite load of female *Psammodromus algirus* lizards. *Canadian Journal of Zoology*, 85(6), 743-751.
- Blumstein, D. T., Fernandez-Juricic, E., Zollner, P. A., & Garity, S. C. (2005). Inter-specific variation in avian responses to human disturbance. *Journal of Applied Ecology*, 42(5), 943-953.
- Broom, M., & Ruxton, G. D. (2005). You can run — or you can hide: optimal strategies for cryptic prey. *Behavioral Ecology*, 16, 534-540.
- Cabido, C., Galan, P., Lopez, P., & Martin, J. (2009). Conspicuousness-dependent antipredatory behavior may counteract coloration differences in Iberian rock lizards. *Behavioral Ecology*, 20(2), 362-370.
- Carretero, M. A., Vasconcelos, R., Fonseca, M., Kaliontzopoulou, A., Brito, J. C., Harris, D. J., & Pererad, A. (2006). Escape tactics of two syntopic forms of the *Lacerta perspicillata* complex with different colour patterns. *Canadian Journal of Zoology*, 84(11), 1594-1603.
- Chapco, W., Martel, R., & Kuperus, W. (1997). Molecular phylogeny of North American band-winged grasshoppers (Orthoptera: Acrididae). *Annals of the Entomological Society of America*, 90(5), 555-562.

- Cuadrado, M., Martin, J., & Lopez, P. (2001). Camouflage and escape decisions in the common chameleon *Chamaeleo chamaeleon*. *Biological Journal of the Linnean Society*, 72(4), 547-554.
- de Barros, F. C., Carvalho, J. E. de, Abe, A. S., & Kohlsdorf, T. (2010). Fight versus flight: the interaction of temperature and body size determines antipredator behaviour in tegu lizards. *Animal Behaviour*, 79(1), 83-88.
- Dewitt, T. J., Sih, A., & Hucko, J. A. (1999). Trait compensation and cospecialization in a freshwater snail: size, shape and antipredator behaviour. *Animal Behaviour*, 58(2), 397-407.
- Endler, J. A. (1978). A predator's view of animal color patterns. *Evolutionary Biology*, 11, 319-364.
- Fernandez-Juricic, E., Jimenez, M. D., & Lucas, E. (2002). Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances for birds in forested habitats. *Canadian Journal of Zoology*, 80(7), 1212-1220.
- Forsman, A., & Appelqvist, S. (1998). Visual predators impose correlational selection on prey color pattern and behavior. *Behavioral Ecology*, 9(4), 409-413.
- Forsman, Anders. (1997). Thermal capacity of different colour morphs in the pygmy grasshopper *Tetrix subulata*. *Annales Zoologici Fennici* (Vol. 34, pp. 145-149).
- Fries, M., Chapco, W., & Contreras, D. (2007). A molecular phylogenetic analysis of the Oedipodinae and their intercontinental relationships. *Journal of Orthoptera Research*, 16(2), 115-125. Allen Press, Inc., 810 East Tenth St. doi:10.1665/1082-6467(2007)16[115:AMPAOT]2.0.CO;2
- Goodman, B. A. (2009). Nowhere to run: the role of habitat openness and refuge use in defining patterns of morphological and performance evolution in tropical lizards. *Journal of Evolutionary Biology*, 22(7), 1535-1544.
- Gutzwiller, K. J., & Marcum, H. A. (1997). Bird reactions to observer clothing color: implications for distance-sampling techniques. *Journal of Wildlife Management*, 61, 935-947.
- Heatwole, H. (1968). Relationship of escape behavior and camouflage in anoline lizards. *Copeia*, 1968, 109-113.

- Hertz, P. E., Huey, R. B., & Nevo, E. (1982). Fight vs. flight: thermal dependence of defensive behaviour in a lizard. *Animal Behaviour*, 30, 676-679.
- Joern, A., & Rudd, N. T. (1982). Impact of predation by the robber fly *Proctacanthus milbertii* (Diptera: Asilidae) on grasshopper (Orthoptera: Acrididae) populations. *Oecologia*, 55(1), 42-46.
- Kuitert, L. C., & Connin, R. V. (1952). Biology of the American grasshopper in the southeastern United States. *The Florida Entomologist*, 35(1), 22-33.
- Langellotto, G. A., & Denno, R. F. (2004). Responses of invertebrate natural enemies to complex-structured habitats: A meta-analytical synthesis. *Oecologia*, 139(1), 1-10.
- Litzenberger, G., & Chapco, W. (2001). A molecular phylogeographic perspective on a fifty-year-old taxonomic issue in grasshopper systematics. *Heredity*, 86(1), 54-59. Blackwell Science Ltd. doi:10.1046/j.1365-2540.2001.00806.x
- McNett, B. J., & Rypstra, A. L. (2000). Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecological Entomology*, 25(4), 423-432.
- Rand, A. S. (1964). Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology*, 45, 863-864.
- Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding attack. The evolutionary ecology of crypsis, warning signals and mimicry*. Oxford: Oxford University Press.
- Song, H., & Wenzel, J. W. (2008). Phylogeny of bird-grasshopper subfamily Cyrtacanthacridinae (Orthoptera: Acrididae) and the evolution of locust phase polyphenism. *Cladistics*, 24(4), 515-542.
- Walther, F. R. (1969). Flight behaviour and avoidance of predators in Thomson's gazelle (*Gazella thomsoni* Guenther 1884). *Behaviour*, 34, 184-221.

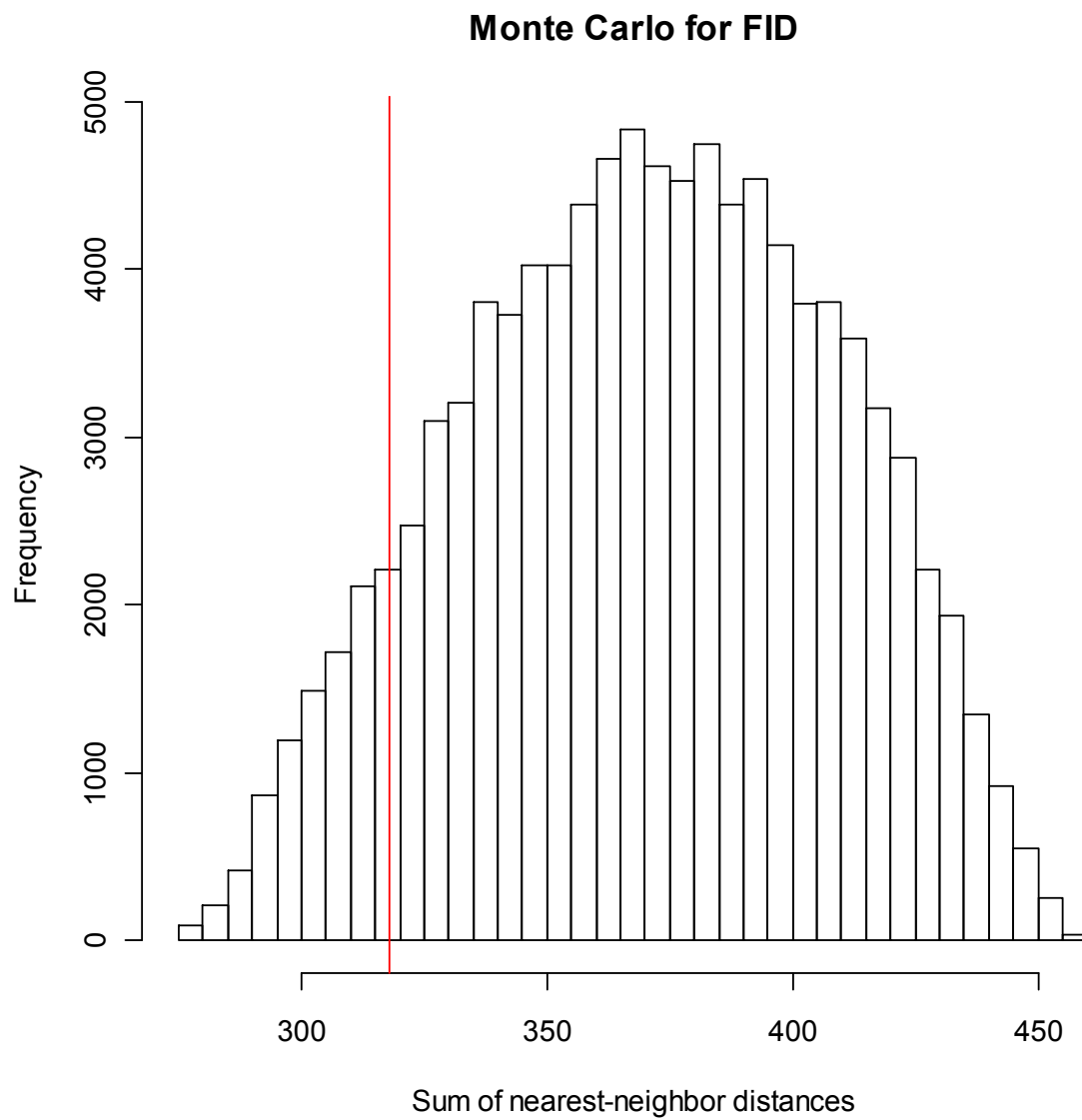


Figure 6.1. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for FID. The true value of the sum of the nearest-neighbor FID distances is marked by the red line.

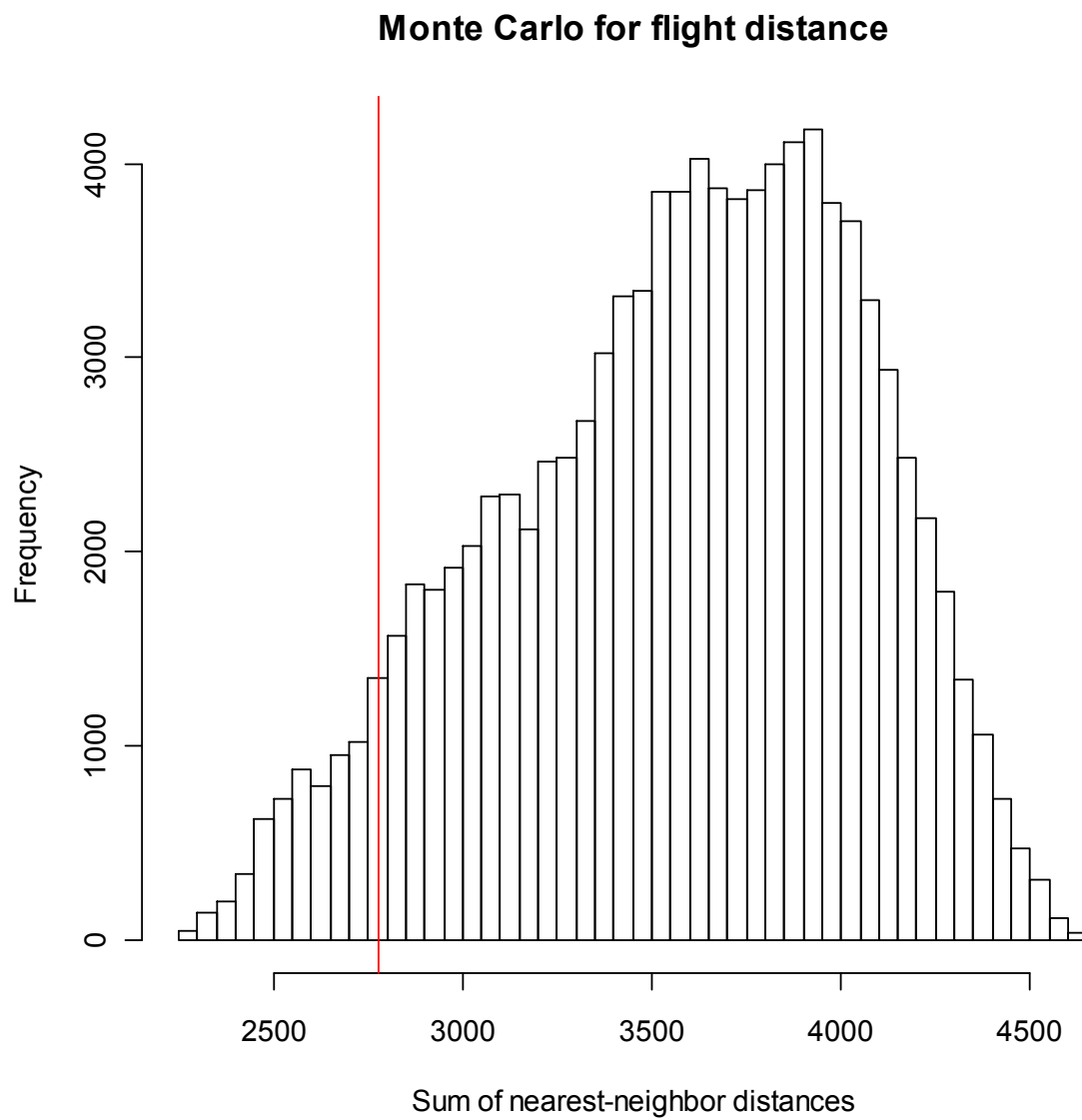


Figure 6.2. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for flight distance. The true value of the sum of the nearest-neighbor flight distances is marked by the red line.

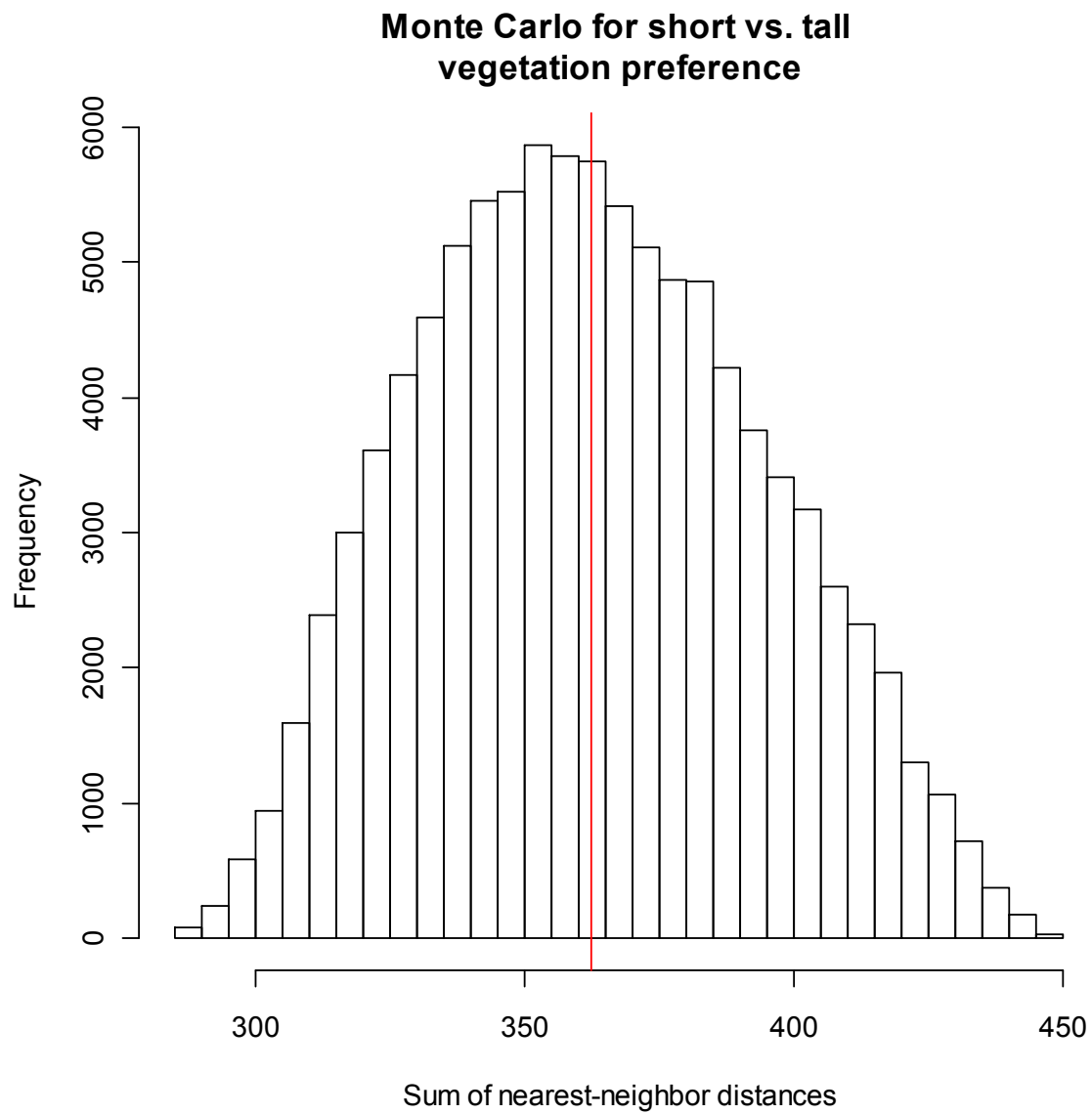


Figure 6.3. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for short-versus-tall vegetation preference. The true value of the sum of the nearest-neighbor short-versus-tall vegetation preferences is marked by the red line.

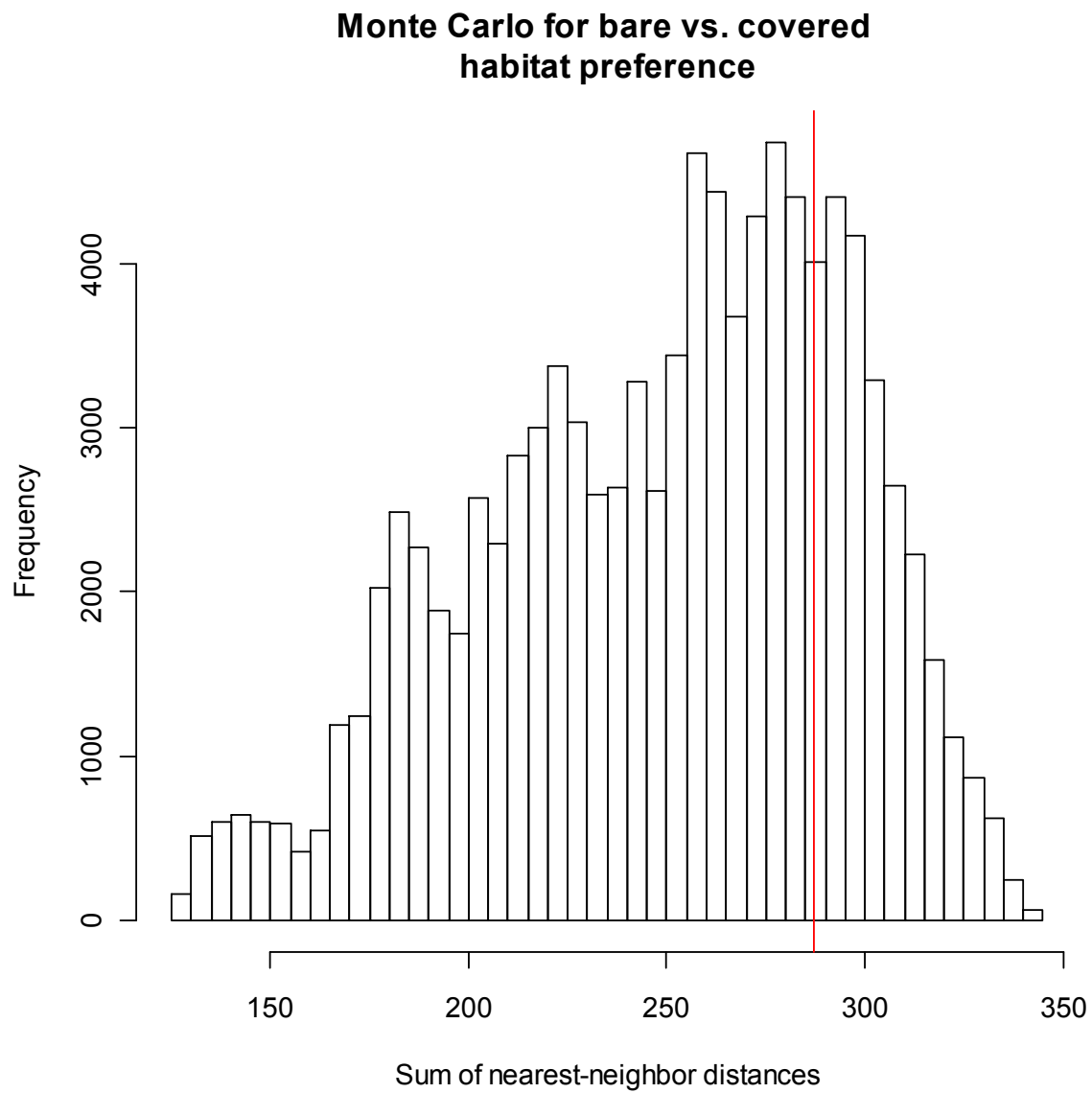


Figure 6.4. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for bare-versus-covered habitat preference. The true value of the sum of the nearest-neighbor bare-versus-covered habitat preferences is marked by the red line.

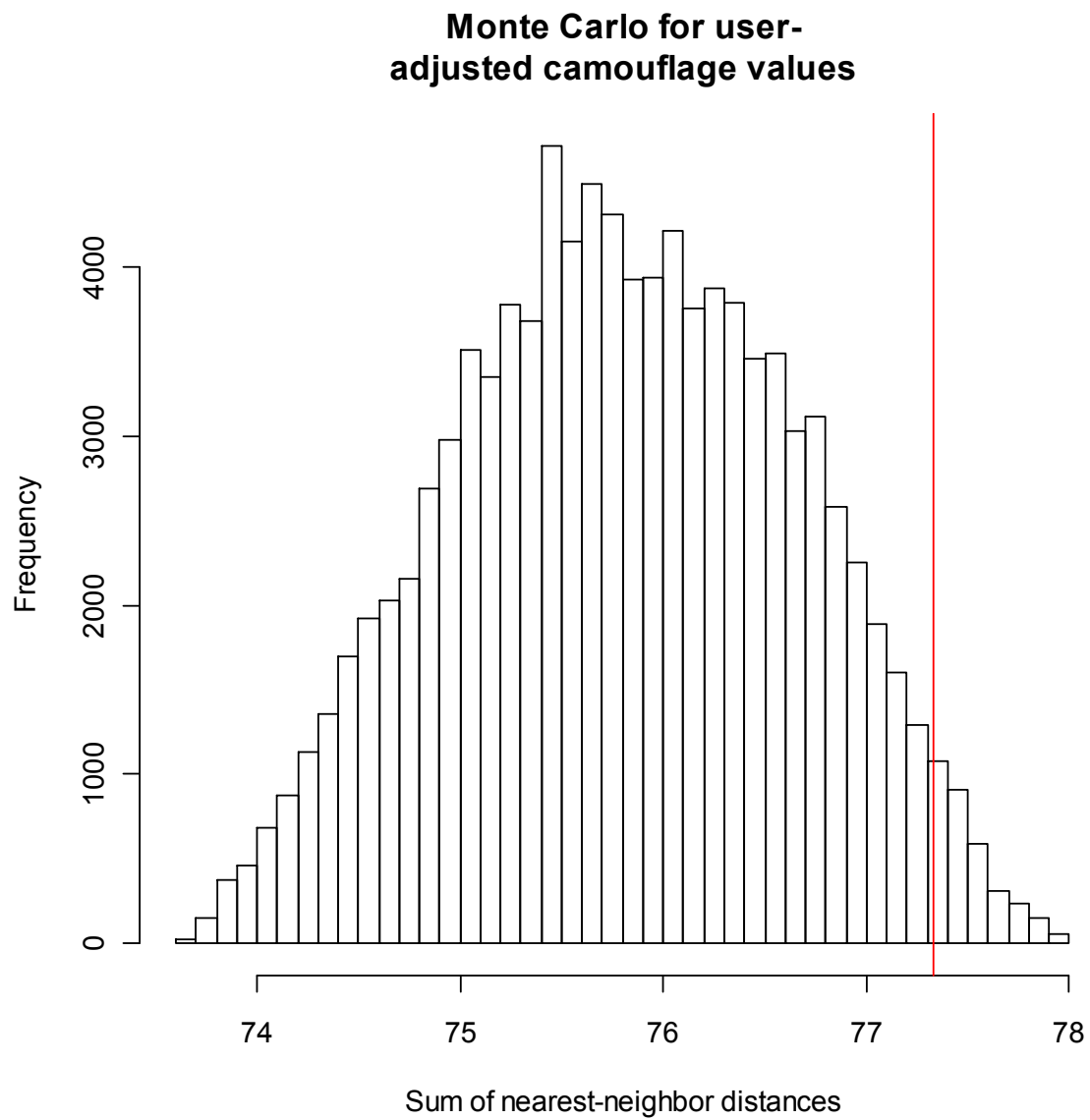


Figure 6.5. Monte Carlo distribution for the sum of the phylogenetic nearest-neighbor distances calculated for camouflage scores adjusted for users. The true value of the sum of the nearest-neighbor camouflage scores is marked by the red line.

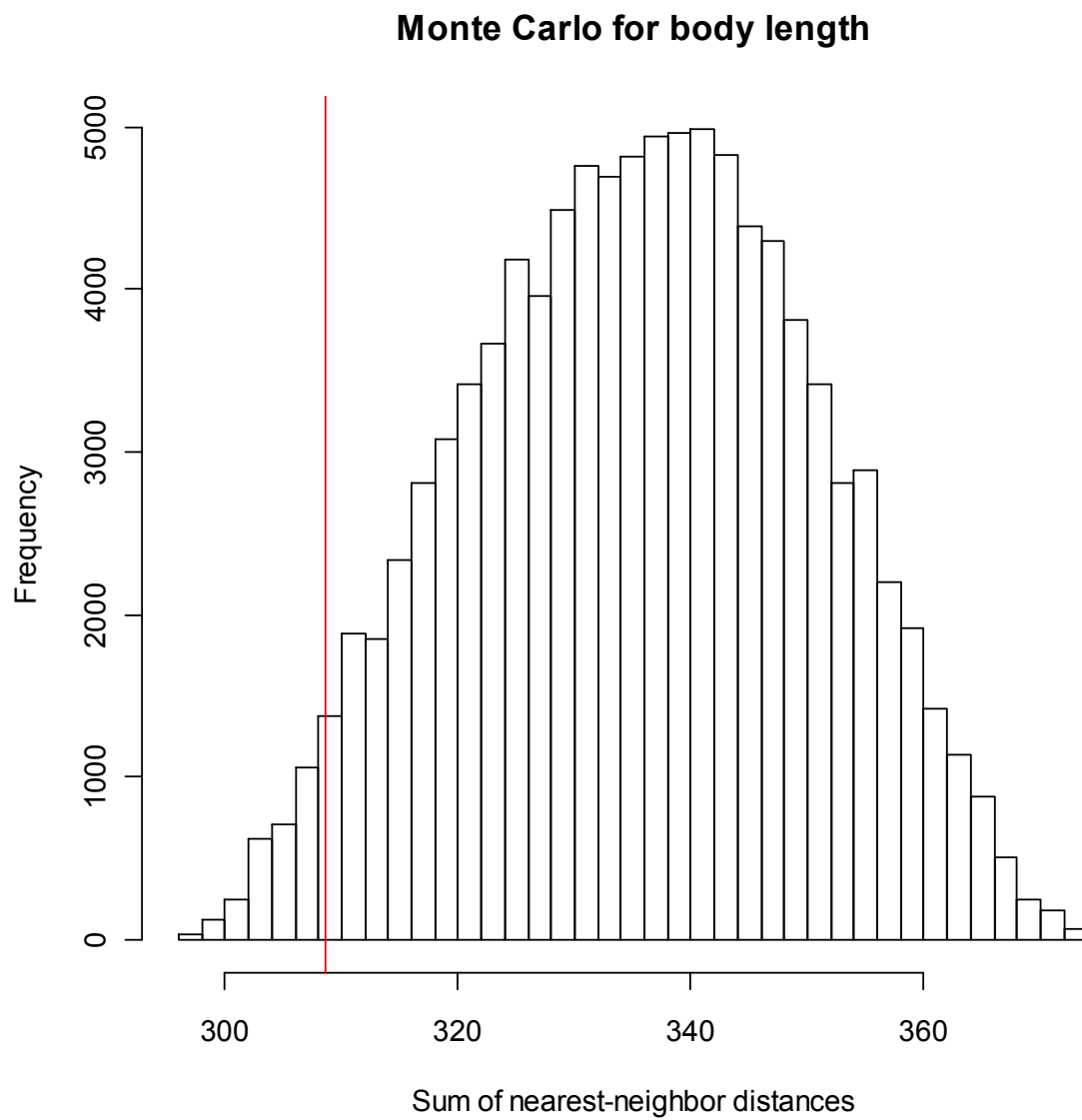


Figure 6.6. The Monte Carlo distribution for sum of the phylogenetic nearest-neighbor distances calculated for body length. The true value of the sum of the nearest-neighbor body lengths is marked by the red line.