

BILATERAL ASYMMETRY IN TWO SECONDARY SEXUAL
CHARACTERS IN THE WESTERN FENCE LIZARD
(*SCELOPORUS OCCIDENTALIS*): IMPLICATIONS
FOR A CORRELATION WITH LATERALIZED
AGGRESSION

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in
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by
Jackson D. Shedd
Spring 2009

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DEDICATION

To Mela



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ABSTRACT

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Three forms of bilateral asymmetry (antisymmetry, fluctuating asymmetry, and directional asymmetry) exhibited by animals have been recognized in the literature. A preference for the use of the left visual field during aggressive intraspecific interactions has been found in a variety of vertebrate taxa. However, correlations between the use of bilaterally asymmetric morphological characters and aggressive displays mediated by neurological asymmetry are not well studied. The western fence lizard (*Sceloporus occidentalis*) exhibits bilateral asymmetry in two secondary sexual characters used in territoriality; blue abdominal signal patches and femoral pores. Abdominal

patches are used in visual communication while femoral pores are used in chemical communication. Here I present data that supports implications for a correlation between visual signaling and left-eye aggression in male *S. occidentalis*. I measured abdominal patch length and femoral pore number for left and right sides of adult male and female lizards from five localities in northern California. The results from this study show that this species collectively exhibits left directional asymmetry (DA) in abdominal patch length across all field sites. Males also showed left DA in patch length separately from females, which were not found to do so. Further, females collectively expressed a significantly higher number of femoral pores on the left hind limb across all field sites, but males did not. However, both male and female voucher specimens examined from one population, the Sutter Buttes, expressed significant left DA in femoral pore number.

CHAPTER I

INTRODUCTION

Bilateral Asymmetry

The majority of animal phyla are characterized by the condition of being bilaterally symmetrical with most notable exceptions being the poriferans, cnidarians, and echinoderms. The so-called Bilateria includes most animals, nearly all of which are bilaterally symmetrical, or approximately so. However, developmental deviations from perfect bilateral symmetry do exist within the Bilateria. These asymmetries among generally symmetrical animals have typically been recognized as three distinct forms; fluctuating asymmetry, antisymmetry, and directional asymmetry (Van Valen, 1962; Palmer and Strobeck, 1986). Fluctuating asymmetry (FA) is characterized by a normal distribution of left biased to right biased trait values with a mean of zero, with zero representing perfect symmetry. Fluctuating asymmetry is thought to occur when development of a normally symmetrical trait is disrupted resulting in slight variation from perfect symmetry. These developmental disturbances often are the result of either environmental or genetic stress factors (Leary and Allendorf, 1989). Antisymmetry refers to situations in which a bilaterally expressed trait is not symmetrically expressed but the direction of the developmental asymmetry varies between left and right side in individuals within a population. A classic biological example of antisymmetry involves the greatly enlarged signaling claw in male fiddler crabs (*Uca* spp.), where one claw is

greatly enlarged relative to the other and is used for defense, and social displays. The enlarged claw occurs with approximately equal frequency on either the right or the left side in nearly all populations of all species (Davis, 1978). The non-directional asymmetry results in a platykurtic (broad peaked) or bimodal distribution of trait values about a mean of zero. In contrast, directional asymmetry (DA) is defined as a consistent bias toward greater development of a bilateral character on one side of the body than on the other (Van Valen, 1962; Palmer and Strobeck, 1986). Examples of this type of asymmetry occur in both invertebrates and vertebrates, including *Erebomyia exalloptera*, a dolichopodid fly with a left wing that is larger and shaped differently than the right (Runyon and Hurley, 2004) and the wrybill (*Anarhynchus frontalis*), a shorebird endemic to New Zealand with a bill tip that is consistently curved to the right used in foraging by means of stone-turning (Davies, 1997). Directionally asymmetric characters show a distribution of trait values that is skewed to the left or right about a mean of zero.

The causes of asymmetry are varied. Fluctuating asymmetry is generally thought to result from random errors in (otherwise) symmetrical developmental processes, which are more common and more extreme if genetic or environmental stressors interfere with normal development. Antisymmetry was originally thought to be “developmentally controlled” and “normally adaptive” (Van Valen, 1962) and later described as having a genetic or developmentally directed foundation (Palmer and Strobeck, 1992). For example, in male fiddler crab claws, one is used for signaling displays and the other for feeding. In the event that the large claw is lost, it is functionally replaced by the smaller (feeding) claw, which grows larger while the original large claw is slowly regenerated as the feeding claw (Morgan, 1924). On the population level any

individual is just as likely to have recently lost its right claw and hypertrophied its left and vice versa. In the case of directional asymmetry there may be a functional or developmental reason for the direction of asymmetry.

The vertebrate brain is divided into two hemispheres which differ in both anatomy and the types of neurobiological tasks that they undertake (Ghirlanda and Vallortigara, 2004). These asymmetries in many cerebral regions correlate with a multitude of different tasks. For example, various bird species (Mench and Andrew, 1986; Güntürkün and Kesh, 1987; Hunt et al., 2001) exhibit a right side bias when handling objects. Other asymmetric hemispheric specializations are known for tasks such as foraging (Franklin and Lima, 2001) and social interactions (Hews and Worthington, 2001) and may be related to the optimization of anti-predator vigilance (Hews et al., 2004). This neurological asymmetry may provide a functional explanation for a variety of morphological asymmetries.

Lateralized Aggression

The two different hemispheres of the vertebrate brain can be specialized (i.e., lateralized) for different functions. This phenomenon is well-recognized and has been exhaustively studied in humans, however lateralization of functionality has been investigated in non-human vertebrate species only within the last few decades (Hews et al., 2004). One behavioral trait that appears to have lateralized functionality is the aggressive responses between conspecifics. Aggressive responses between conspecifics have been shown to be coupled with a left visual field bias in a diverse number of vertebrate taxa (Hews and Worthington, 2001). The anurans *Bufo marinus* (Robins et al.,

1998; Vallortigara, 2000) and *Litoria caerulea* (Robins and Rogers, 2006), domestic fowl (*Gallus gallus*) (Rogers et al., 1985; Bullock & Rogers, 1986), baboons (*Theropithecus gelada*) (Casperd and Dunbar, 1996) and various lizard species (Deckel, 1995; Deckel, 1998; Deckel and Jevitts, 1997; Hews and Worthington, 2001; Hews et al., 2004) have all been show to display lateralized left-eye aggression.

Under laboratory conditions, Deckel (1995; 1998) and Deckel and Jevitts (1997) found that male green anoles (*Anolis carolinensis*) favor the use of their left eye during agonistic encounters, suggesting that this species mediates aggressive responses predominantly through right-hemispheric brain mechanisms. During studies in natural conditions, it was subsequently observed that male ornate tree lizards (*Urosaurus ornatus*) (Hews and Worthington, 2001) and female striped plateau lizards (*Sceloporus virgatus*) (Hews et al., 2004) also function more effectively from the right hemisphere of the brain with increased levels of aggression exhibited during intraspecific left visual field encounters. Due to posteriolateral placement of the eye in lizards, binocular vision is prevented in agonistic encounters, and therefore only one side of an opponent's body is ever viewed at a given moment. This lateralized aggression suggests the prediction that morphological characteristics associated with intraspecific encounters may show a pattern of directional asymmetry.

Visual and Chemical Communication in Lizards

Visual cues are an important part of communication in many lizards (Noble and Bradley, 1933; Carpenter, 1978). Visual communication has been well studied in several lizard model systems including *Amphibolurus* (Ord et al., 2002), *Anolis*

(Greenberg and Noble, 1944; Echelle et al., 1971; Stamps, 1973; Sigmund, 1983; Losos, 1985; Lovern et al., 1999; Macedonia and Clark, 2003), *Bradypodion* (Stuart-Fox et al., 2007), *Chamaeleo* (Bustard, 1967; Cuadrado, 1998), *Crotaphytus* (Husak, 2004), *Ctenophorus* (LeBas and Marshall, 2000), *Draco* (Mori and Hikida, 1994), *Eumeces* (Cooper and Vitt, 1988), *Gambelia* (Tollestrup, 1983), *Hemidactylus* (Marcellini, 1977; Regalado, 2003), *Holbrookia* (Cooper, 1984; 1986), *Iguana* (Hazlett, 1980; Phillips, 1995), *Phrynosoma* (Tollestrup, 1981), *Uma* (Carpenter, 1963; 1967), *Urosaurus* (Thompson and Moore, 1991; Carpenter, 1995; Quinn and Hews, 2000; Hews and Bernard, 2001), *Uta* (Sinervo and Lively, 1996; Alonzo and Sinervo, 2001), *Sceloporus* (Ferguson, 1973; Ruby, 1977; Carpenter, 1978; Cooper and Burns, 1987; Martins, 1993; Martins, 1994; Hews and Bernard, 2001) and many others. The western fence lizard (*Sceloporus occidentalis*) is a member of the sister genus to *Urosaurus* and is a sister species to *S. virgatus* (Reeder and Wiens, 1996; Wiens, 1999). Males of these two genera typically exhibit colorful gular and abdominal patches that are used in similar postural signaling displays, characterized by species-specific display action patterns (Carpenter, 1978). The body is compressed ventrolaterally, resulting in the display of the abdominal patches in a conspicuous manner. Competing males of both genera align laterally in a head-to-tail orientation during agonistic interactions so that the side of the body presented and the visual field used is the same for both individuals. Display action patterns elicited by both genera to make the abdominal and gular patches more conspicuous during intraspecific encounters include the head-bobbing or shudder display, the push-up display, and the full-show display (Davis and Ford, 1983; Quinn and Hews, 2000; Hews and Bernard, 2001). In the shudder display, the head is vigorously bobbed up and down

with the dewlap extended and gular patch completely exposed. This display is generally executed while a male pursues a female prior to copulation. The pushup display is characterized by the repeated up and down motion of the anterior portion of the body by extending and retracting the forelimbs, combined with lateral abdominal compression to display the abdominal patches. During full-show, the most conspicuous display, the entire body is repeatedly elevated and lowered by extending and retracting all four limbs, while the body is ventrolaterally compressed, dramatically exposing the entire abdominal patch to the opposing conspecific.

Females give a rejection display towards males that includes exposing the abdominal patches; the back is arched and the body compressed ventrolaterally while the female hops sideways with the distal portion of her tail raised. The gular and abdominal patches develop with sexual maturation and exhibit little or no seasonal variation in expression (Hews and Quinn, 2003). These patches are of various shades of blue in many populations of *S. occidentalis*. This characteristic is responsible for giving the species its common nickname “blue-belly lizard” (Figure 1).

Several types of skin pigment cells, or chromatophores, make up the color patterns expressed in animals (Cooper and Greenberg, 1992; Hews and Quinn, 2003). Of the various types of dermal chromatophores present in abdominal patches of iguanid lizards, iridophores are responsible for the blue color and hue (Morrison et al., 1996). Iridophores are located beneath the epidermal layer and do not contain pigments, but rather, numerous intracellular platelets, which selectively reflect blue wavelengths through interference (Hews and Quinn, 2003). These platelets are often composed of guanine. The coloration and hue of the abdominal patches in *S. occidentalis* is visually



FIG. 1. Examples of sexual dimorphism and asymmetry in the abdominal patches of an adult male (left) and adult female (right) *Sceloporus occidentalis*. The male exhibits a longer left patch, while the female exhibits a longer right patch. Note that limbs are parallel to one another.

received by conspecifics via four retinal cone types; humans have three cone types.

Sceloporus lizards appear to be capable of distinguishing hue well into the blue end of the wavelength spectrum (Loew and Fleishman, unpublished data cited in Hews and Quinn, 2003) and may be capable of visually detecting ultraviolet (UV) light (Stoehr and McGraw, 2001).

In addition to visual signals, many iguanid lizards also use chemical cues for communication (Duvall, 1979; Duvall, 1982; Alberts, 1989; Alberts, 1993; López et al., 1998; Martín and López, 2000; Hews and Bernard, 2001; Sherbrooke, 2003). For example, Werner et al. (1987) showed that green iguanas (*Iguana iguana*) are capable of recognizing their own kin using chemical cues only. Further, feces and secretions from proctodeal and femoral glands have shown to elicit significant responses such as substrate

licking and pushup displays in *S. occidentalis* (Duvall, 1979). Such chemically transmitted signals may significantly aid in territorial advertisements and intraspecific recognition over longer periods than visual display signals (Alberts, 1990) because visual displays are limited by sightlines, visual range, and obstructing features (i.e., vegetation, boulders) and do not last longer than the time taken to deliver them (Alberts, 1993).

Chemical signaling among iguanid lizards is generally delivered by smearing waxy secretions generated in the femoral glands. Intraspecific chemical reception is achieved through tongue-flicking and licking of surface areas where femoral gland secretions have been deposited (Duvall, 1979; Duvall, 1982; Alberts, 1989). These specialized exocrine glands are controlled by androgenic hormones (Fergusson et al., 1985; Alberts, 1991) and release a glandular secretion composed of lipids and proteins through pores running along the femoral region of the underside of the hindlimbs (Cole, 1966; Alberts, 1990; Alberts, 1993). These pores are expressed similarly in immature individuals but are sexually dimorphic in adults with males typically having larger, more conspicuous pores than females in most species. The number of femoral pores has been shown to be asymmetric in some populations of lizards (Martín and López, 2000). Secretory activity is greatest during the breeding season and males produce more secretions than females (Cole, 1966). Morphological location of the femoral pores suggests a passive deposition of the secretions as lizards move through their home ranges (Maderson, 1972; Alberts, 1993) (Figure 2).

Although some recent work has examined femoral pore secretions, overall the function and role of femoral pores is not well understood. Alberts (1993) suggested that the low volatility of femoral gland secretions in desert iguanas (*Dipsosaurus dorsalis*)



FIG. 2. Sexual dimorphism in femoral pores of female (above) and male (below) *Sceloporus occidentalis*.

would limit their function as strictly olfactory cues thus necessitating detection by licking and tongue flicking. However, Alberts (1989) also showed that the secretions strongly absorb long wave UV light (invisible to humans but visible to lizards with their enhanced UV detection ability imbued by their four pigment cone), which may aid in acting as a long-range visual cues to conspecifics that can then be investigated chemically at short range either by olfaction or taste. The number of femoral pores varies greatly both within and among species (Cole, 1966). Femoral pore count for *S. o. occidentalis* ranges from

eleven to twenty-one (Bell and Price, 1996). The waxy, finger-like secretory projections from the femoral pores of male *S. occidentalis* are most evident during the mating season. These are presumably deposited onto surfaces within a territory where conspecifics interpret and react to them, as indicated by behaviors exhibited by both sexes of this species in studies by Duvall (1979; 1982). Martín and López (2000) found a correlation with femoral gland secretions and female mate choice in the non-iguanid lizard *Lacerta monticola*. Females favored associating with scents of males with low fluctuating asymmetry in femoral pore count and also with the scents of males exhibiting a higher number in femoral pore count. Presumably, the females made these discriminations and detected fluctuating asymmetry in male pores based on chemical signals alone.

Natural History of the Western Fence Lizard

The western fence lizard (*Sceloporus occidentalis*) (Iguanidae) is a common to abundant species distributed throughout most of California, Oregon, and Nevada as well as parts of Washington, Idaho, Utah, and northern Baja California. A habitat generalist, *S. occidentalis* is found in most biotic communities within its range excluding the more arid Mojave and Sonoran Deserts, from sea level up to 3,300 m (~10,800 ft) (Bell and Price, 1996; Stebbins, 2003). Up to six subspecies are currently recognized, at least one of which, the insular form *S. o. becki*, probably should be recognized as a distinct species (Wiens and Reeder, 1997; Bell, 2001). This study was conducted within the range of the northwestern fence lizard (*S. o. occidentalis*), which occurs from central Washington south through eastern Oregon and most of northern California including the San Francisco Bay Area, northern San Joaquin Valley, and central Sierra Nevada. It is the

second most widespread form and occurs within the area of this study (Butte, Sutter, and Lassen Counties).

The northwestern subspecies reaches snout-to-vent lengths (SVL) of up to 84mm in males and 80mm in females and is considered sexually monomorphic in size relative to other subspecies (Bell and Price, 1996). However, *S. o. occidentalis* exhibits marked sexual dichromatism. Males are flecked with blue or blue-green dorsally and have prominent dark blue gular and abdominal patches. The gular patch is often preceded anteriorly by black or gray and the abdominal patches are bordered medially by black. In females, the blue gular and abdominal patches are usually present but reduced in size and lighter in color. The rest of the belly is white and the black medial lining of the abdominal patches is typically absent or highly subdued. Females also typically exhibit cryptic dark dorsal chevrons which resemble bark. Overall dorsal coloration in both sexes varies from shades of brown to grayish or reddish to nearly black upon emergence from an inactive state prior to obtaining optimum body temperature (Figures 3 and 4).

Adults become active as early as January at lower elevations (pers. obs.), although February is the typical month for the beginning of activity. Juveniles may be observed basking throughout winter as long as temperatures are warm enough (pers. obs.), as their higher surface area to volume ratio facilitates more rapid energy absorption from the sun. By late June adult lizards at lower elevations begin to restrict their activity greatly due to heat, staying active for only a few hours in the morning before temperatures become unfavorable, and then becoming active again for a few hours in the late afternoon. At higher elevations, brumation may last from October to late March or April. Mating typically begins soon after emergence from brumation and lasts through



FIG. 3. Adult female (above) and male (below) *Sceloporus occidentalis* from Butte Co., CA.

June or into July, depending on elevation and latitude. Oviposition occurs from April to June and as many as three clutches may be produced in a single season, containing from three to seventeen eggs (Davis, 1980; Stebbins, 2003). Hatchlings usually appear in August or September (Davis, 1980; pers. obs.). This species is insectivorous throughout ontogenetic development.



Fig. 4. Adult female (above) and male (below) *Sceloporus occidentalis* from Lassen Co., CA.

Home range size varies based on a number of factors including age, sex, locality, time of year, and food availability (Davis and Ford, 1983; Sheldahl and Martins, 2000). During the mating season, *S. o. occidentalis* hold territories within home ranges, which are defended using visual, chemical, and physical means of communication. Male territories typically overlap with at least one other male (Sheldahl and Martins, 2000).

Males defend territories vigorously from other males (Davis and Ford, 1983) and advertise from prominent perches via postural displays that reveal the blue signal patches on the abdomen. Physical contact may ensue in male-male interactions by means of biting at the opponent's abdominal patches and other areas of the body and holding on (Sheldahl and Martins, 2000; pers. obs.). Female-female interactions are not well-understood (D. Hews, pers. comm.), however postural displays by females towards males occur frequently (pers. obs.). Chemical signals secreted by femoral pores, located on the ventral surface of the thigh in both sexes, are used in territoriality as well (Duvall, 1979).

Many species prey on *Sceloporus occidentalis* throughout its distribution due to its small size and conspicuous diel activity patterns. These predators include many bird and mammal species, snakes, and other lizards (Bell and Price, 1996 and references therein). Bury (1972) reported on predation by a giant salamander (*Dicamptodon ensatus*, sensu lato). As with most iguanid lizards, the tail can be autotomized in evading predation or during intraspecific combat and then regenerated.

Statement of Research Investigation

Both external morphology (Møller, 1994; Alvarez, 1995; Bowyer et al., 2001; Kark, 2001) and neuroanatomy of the cerebral hemispheres (Mench and Andrew, 1986; Güntürkün and Kesh, 1987; Deckel, 1995; Hews and Worthington, 2001; Hunt et al., 2001) can be directionally asymmetric in many vertebrate species. However, correlations between morphological and neurological asymmetries relating to aggression are not well-studied. Iguanid lizards show the potential to serve as excellent models for the study of neurological and morphological asymmetries. They are conspicuous, abundant, easy to

observe in most environments, and exhibit asymmetric behaviors, such as lateralized aggression that may reasonably be expected to be connected with asymmetry in conspicuous external morphological features (i.e., abdominal patches). For my primary thesis research I tested the hypothesis that the size of a secondary sexual character, the abdominal signaling patches, in *S. occidentalis* would differ in relation to the more frequently displayed left side of the body. A prediction from this hypothesis is that abdominal signaling patches on the left side of the body in this species would be larger than those on the right side, based on the tendency to favor the left visual field during intraspecific aggression. I also hypothesized that the number of femoral pores, an additional secondary sexual character, would be greater on the left hind limb than on the right. This is due to evident asymmetry in this trait within this species and such asymmetries observed in femoral pores have been shown to have significant effects on lizard social systems (Martín and López, 2000).

Hypotheses Tested

For this study, I tested the hypothesis that there is a difference in the length of the left and right abdominal patch based on neurological asymmetries exhibited by *Sceloporus occidentalis*. I also tested the hypothesis that there is a difference in the number of femoral pores between the left and right hind limbs based on neurological asymmetries exhibited by *S. occidentalis*. From these hypotheses, a number of predictions (P) were made, which are outlined below:

□ P₁: Abdominal patch length is greater on the left side than on the right in *S. occidentalis*.

- ❑ P₂: Male and female *S. occidentalis* differ in the degree and frequency of abdominal patch asymmetry.
- ❑ P₃: Asymmetry differs in abdominal patch length amongst similar-sized male *S. occidentalis*.
- ❑ P₄: Femoral pore number is greater on the left hind limb than on the right in *S. occidentalis*.
- ❑ P₅: Male and female *S. occidentalis* differ in the degree and frequency of femoral pore asymmetry.
- ❑ P₆: There is a correlation between asymmetry in femoral pore count and abdominal patch length in *S. occidentalis*.

CHAPTER II

METHODS

Study Sites

Field sampling for this study was conducted during the breeding season from the beginning of April, 2008 through July 1, 2008 at the Big Chico Creek Ecological Reserve (BCCER) and the Butte Creek Ecological Preserve (BCEP) where data were collected from 82 and 55 lizards, respectively (Figure 5). Forty-one lizards were also sampled from a site at Eagle Lake, Lassen County from June 21 to 23, 2008.



FIG. 5. Butte Creek Ecological Preserve (BCEP) field site at 91m, Butte Co., California. Photograph courtesy of Julie Nelson.

The BCCER is relatively pristine and located in the Big Chico Creek watershed, Butte County, California. It consists of approximately 1,619 hectares (4,000 acres) composed of chaparral, riparian, oak savannah, mixed oak woodland, and pine-oak woodland. Two sites were selected here along a north-south gradient of the creek in the bottom of Big Chico Creek Canyon, herein referred to as BCCER North and BCCER South. The two sites are separated by a distance of 3.2 km (2 mi). BCCER North is at an elevation of 274m (~900 ft) in an oak woodland clearing along the creek, the predominant oak species being canyon live oak (*Quercus chrysolepis*). Incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*) are most common on the Reserve at this site's elevation. BCCER South is at an elevation of 244m (~800 ft) in an open clearing along the creek within mixed oak woodland composed of canyon live oak (*Q. chrysolepis*), blue oak (*Q. douglasii*), valley oak (*Q. lobata*), and interior live oak (*Q. wislizenii*). Gray pine (*Pinus sabiniana*) is also present, and willow (*Salix* sp.) and California buckeye (*Aesculus californica*) are common at this site. Both BCCER sites had ample amounts of river rock, boulders, and logs for basking (Figures 6 and 7).

The BCEP is regarded as a disturbed site. It is located in the Butte Creek watershed at an elevation of 91m (~300 ft) and consists of some 38 hectares (93 acres), including more than a mile stretch of Butte Creek. Mining, invasive plant introductions, and human habitation in close proximity have had substantial environmental impacts this site. Vegetation is diverse here; gray pine (*Pinus sabiniana*), western sycamore (*Platanus racemosa*), Fremont's cottonwood (*Populus fremontii*), willow (*Salix* spp.), blue elderberry (*Sambucus mexicana*), and oak (*Quercus* spp.) predominate. Some flourishing

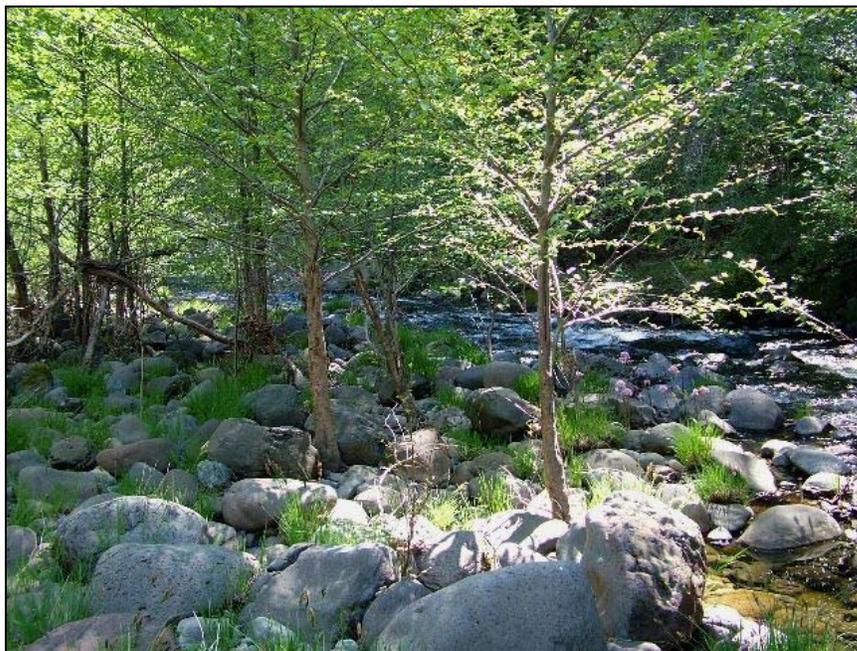


FIG. 6. Big Chico Creek Ecological Reserve North (BCCERN) field site at 274m, Butte Co., California.

invasive plants include tree-of-heaven (*Ailanthus altissima*), yellow star-thistle (*Centaurea solstitialis*), Scotch broom (*Cytisus scoparius*), and Himalayan blackberry (*Rubus discolor*). Abundant sources for basking throughout this site include river rock, scattered boulders, logs and other woody debris, and artificial structures (e.g. storage shed, wood benches, interpretative kiosk).

Eagle Lake is the second largest natural lake entirely within California state borders. It is located in Lassen County at an elevation of 1,558 m (5,112 ft), approximately twelve miles (by air) north of Susanville. Lizards were sampled along a stretch of the east shore with CSU, Chico's Eagle Lake Field Station (ELFS) as a central location (Figure 8). Habitat at this site is characterized by abundant basalt lava rock and boulders lining the lake shore. Predominant vegetation is comprised of big sagebrush

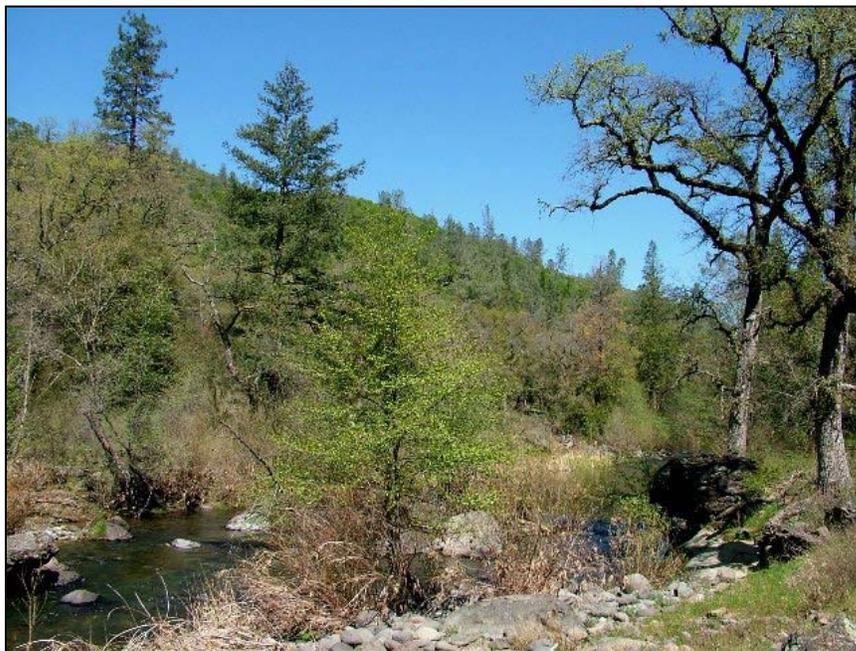


FIG. 7. Big Chico Creek Ecological Reserve South (BCCERS) field site at 244m Butte Co., California.

(*Artemisia tridentata*), western juniper (*Juniperus occidentalis*), and pine (*Pinus jefferyi* x *P. ponderosa*). *Sceloporus occidentalis* at this site appear to be exclusively saxicolous (pers. obs.). This is the only field site within this study where *S. occidentalis* is sympatric with the sagebrush lizard (*S. graciosus*).

Museum Sampling

An additional 200 specimens of *S. occidentalis* (N =100 males; N =100 females) from the Sutter Buttes, Sutter County, CA were sampled for femoral pore count measurements from the California State University, Chico Vertebrate Museum collection. Abdominal patch measurements were not taken due to the contorted form of the lizards, faded edges of the patches, and dismembered torsos where stomach contents had been



FIG. 8. Eagle Lake Field Station (ELFS) site at 1,558 m, Lassen Co., California.

removed. This is the only other region in this study where *S. occidentalis* is sympatric with *S. graciosus*.

Sampling Design

I collected all data in an effort to standardize procedures and eliminate any possible bias. Aid in the field by others was strictly for the capture and release of lizards and recording data as lizards were processed.

Abdominal Patch Measurements

Sexually mature lizards (≥ 55 mm SVL) were noosed or, on occasion, caught by hand. Early in the study (April) lizards could be caught throughout the day, with measurements taken intermittently. As daily temperatures increased in May, all adult lizards that could be captured in the morning hours were placed in a large container prior

to processing. An effort was made to keep the contained lizards at a moderate temperature to keep them from over-heating or from getting too cool; changing temperatures affect the integrity of abdominal patch color and intensity (Morrison et al., 1996; pers. obs.). Left and right patch designation morphologically correlated with left and right eye visual fields (Figure 9).

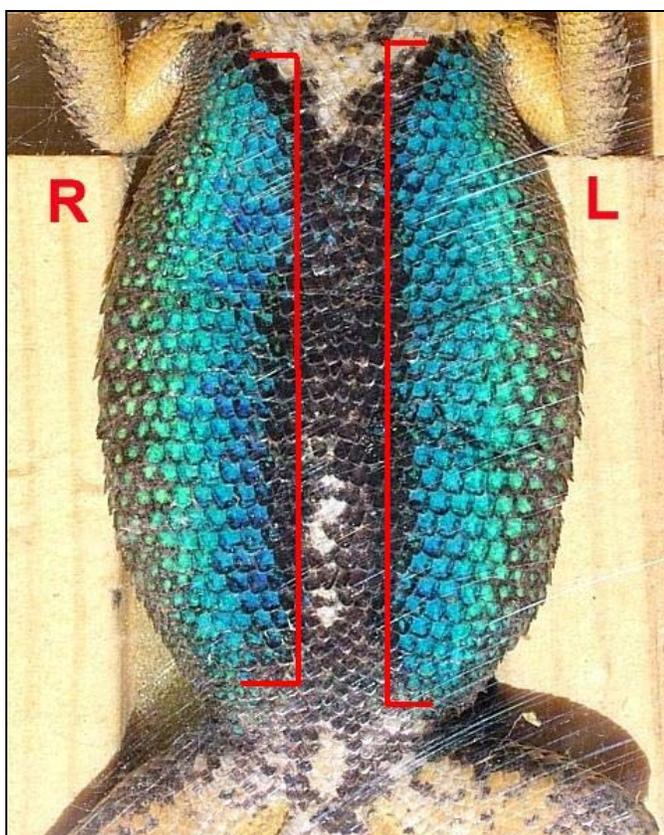


FIG. 9. Abdominal patch lengths were determined by the number of scale rows from the anterior-most scale with any amount of blue to the posterior-most scale with any amount of blue connected by the number of contiguous solid blue scales in between. Right patch length = 32 rows and left patch length = 35 rows for the individual pictured. “R” and “L” designate right and left patches corresponding to the lizard’s morphology.

Lizards were individually positioned on their backs on a foam-lined wood block ('the cradle') (Figure 10) under a Fujifilm FinePix S7000 digital camera mounted on a stand for photographs of the abdominal patches. The transparent plastic cover of a CD case was placed over the lizard's belly in order to spread the abdominal patches and create a flat plane. Three to four photographs were taken both in the sun and in shade depending on how high the sun was and how much glare reflected off the CD case cover.



FIG. 10. "The cradle" upon which lizards were mounted for photographic processing.

The camera was mounted onto a 9 x 11.5cm piece of wood connecting to a 28.75cm aluminum stand, bolted to a 30.5 x 30.5cm base board (Figure 11). The camera was easily mounted and dismounted with a 0.25" x 0.50" thumb screw. The "cradle" structure was a 4.5 x 4.5 x 2cm block of wood with a 2.25cm wide groove running the



FIG. 11. Camera mounted to stand for photographic processing in the field.

length of it. A thin piece of foam was laid over the grooved depression in the wood block, which conformed to a lizard's back while the plastic cover was placed over it. Lizards were positioned so that the head hung off the cradle and so their forelimbs could be kept spread while under the CD case cover (Figure 12).

Digital photographs were enlarged in Adobe Photoshop CS 8.0 and the blue scales comprising the length of each abdominal patch were individually counted.

Patch length was determined by the number of contiguous blue scales counted from the anterior-most scale with any amount of blue to the posterior-most scale with any amount of blue (Figure 9). Clearly, to obtain an evaluation of abdominal patch length or

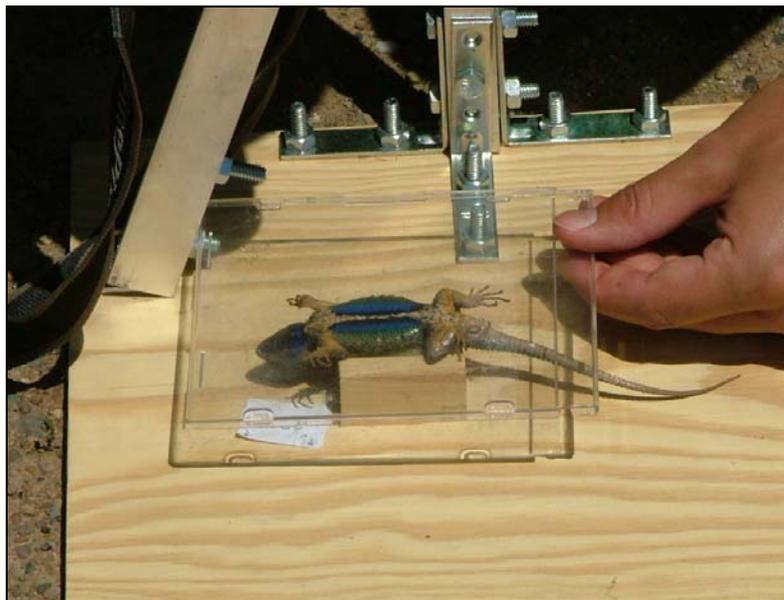


FIG. 12. A male *Sceloporus occidentalis* mounted under plastic CD case cover for abdominal patch photographs.

total surface area for each patch it might initially appear sensible to employ the advanced methods of geometric morphometric analysis or other such programs; however, due to the plastic nature of the abdominal skin, and shifting of the lizard's position while being photographed, a scale count for patch length proved to be the most precise measurement.

Femoral Pore Measurements

A femoral pore count was taken in the field by quantifying the number of pores on each leg. The count was taken at least twice to ensure a correct count. For females many counts were often necessary for a confident quantification, as the pores are significantly smaller. Femoral pores of many of the museum specimens were inconspicuous due to length of preservation time and scale flaking, particularly those of females. Therefore, a light-powered Leica S6E dissecting microscope was used to quantify pores in both males and females.

Other Collected Data

Toes were clipped using a standard method (Figure 13) to ensure that recaptures at each site were not reprocessed. Lizards were numbered exponentially with respect to what number they were caught within the study. One to four digits from different feet were clipped for a sum relative to the number of the lizard being processed. In addition, measurements for SVL were taken for all lizards in the field.

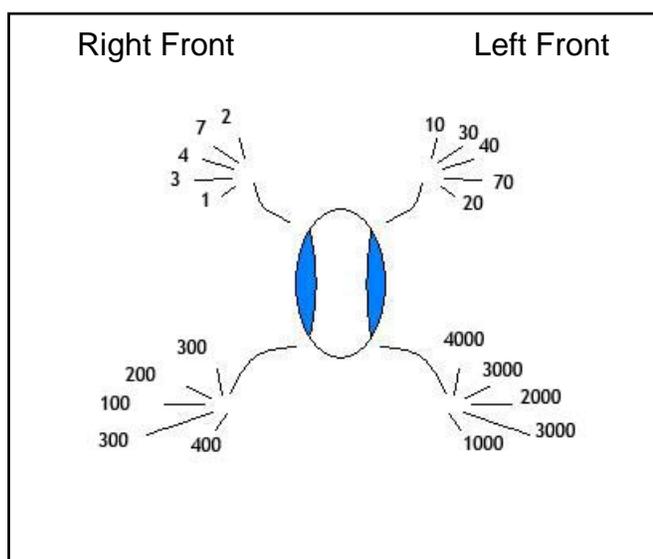


FIG. 13. Toe clipping methodology for marking lizards to ensure individuals were only measured once upon subsequent visits to each field site. Diagram depicts lizard in belly-up position.

Statistical Analyses

All data for this study were analyzed using JMP Statistical Software (SAS Inc.), Version 8.0 and STATISTICA (StatSoft, Inc.) Version 6.0. I used log transformation and a Shapiro-Wilk test to ensure data normality. The procedures for which various analyses were performed are discussed below.

Abdominal Patch Asymmetry

First, it was determined whether the left patch was greater than the right patch in length for all lizards and between sexes across all field sites. These analyses were done with a one-tailed paired t-test using left minus right (L-R) differences for patch length measurements. To determine if left patch length was greater than the right between field sites a one-way Analysis of Variance was used. This analysis was also performed to determine if left patch length was greater than right between sexes, between field sites.

A regression was used to investigate whether or not abdominal patch length in males was more asymmetric with greater patches in relation to SVL than those with smaller patches. This was determined by taking an average of left and right patch size divided by SVL against the difference in left and right patch length. Males with SVL of 65mm or greater were classified as “similar.” Smaller males (SVL <65mm) were not included in the regression.

Femoral Pore Asymmetry

First, it was determined whether the number of femoral pores on the left hind limb was greater than that of the right with a one-tailed paired t-test using the L-R differences between the number of pores on each leg. This test was performed for the overall total number of lizards and between sexes across field sites. This test was also performed for lizards from the Sutter Buttes. A one-way Analysis of Variance was used to determine if the number of femoral pores was greater on the left hind limb than on the right between field sites (including differences between sexes between field sites).

A simple regression was used to determine if a correlation between pore number on the left limbs and left abdominal patch length existed.

CHAPTER III

RESULTS

Abdominal Patch Asymmetry

Left patch length was found to be significantly greater than right patch length at the α 0.10 level for all lizards among all sites ($p=0.0781$). Further, males were found to have significantly greater left patch length over right patch length ($p=0.01$), while females were not ($p=0.387$) (Figures 14 and 15).

Abdominal patch length for all lizards showed no significant differences between sites except those from ELFS at the α 0.10 level (BCEP: $p=0.20$; BCCER N: $p=0.33$; BCCER S: $p=0.24$; ELFS: $p=0.072$) (Figure 16).

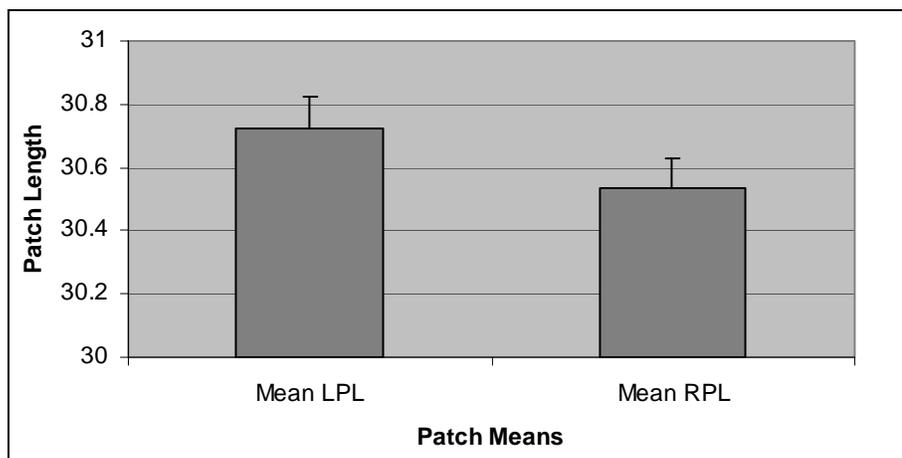


FIG. 14. Differences in mean values for left patch length (LPL) and right patch length (RPL) for all lizards among all field sites (BCEP, BCCER N, BCCER S, ELFS). Standard error bars are included.

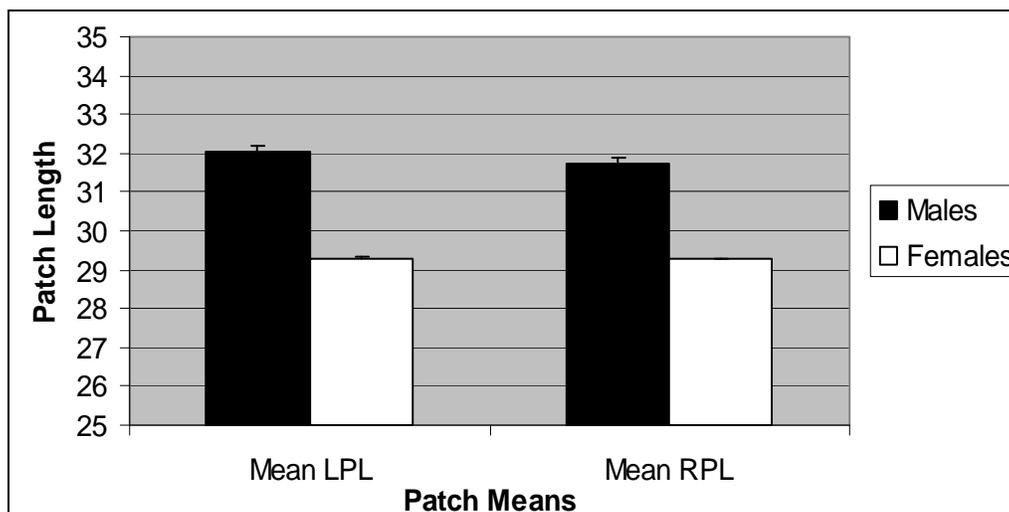


FIG. 15. Differences in mean values for left patch length (LPL) and right patch length (RPL) between sexes among all field sites. Standard error bars are included.

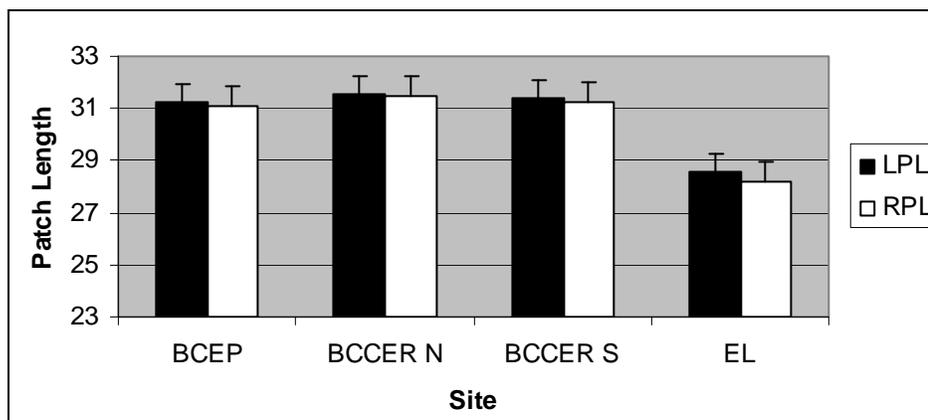


FIG. 16. Differences in mean values for left patch length (LPL) and right patch length (RPL) for all lizards between field sites. Standard error bars are included.

A one-way Analysis of Variance was used to determine the difference in abdominal patch length between field sites and between sexes. Left patch length was

found to be significantly greater than right in males at BCCER S ($p=0.0162$) with a tendency shown for males at BCCER N ($p=0.103$). Left patch length in males at BCEP and ELFS were found to be insignificant ($p=0.2243$ and $p=0.197$, respectively). Females showed no significant results, though a tendency was shown for ELFS (BCCER N: $p=0.80$; BCCER S: $p=0.65$; BCEP: $p=0.37$; ELFS: $p=0.13$) (Figures 17 and 18, Tables 1 and 2).

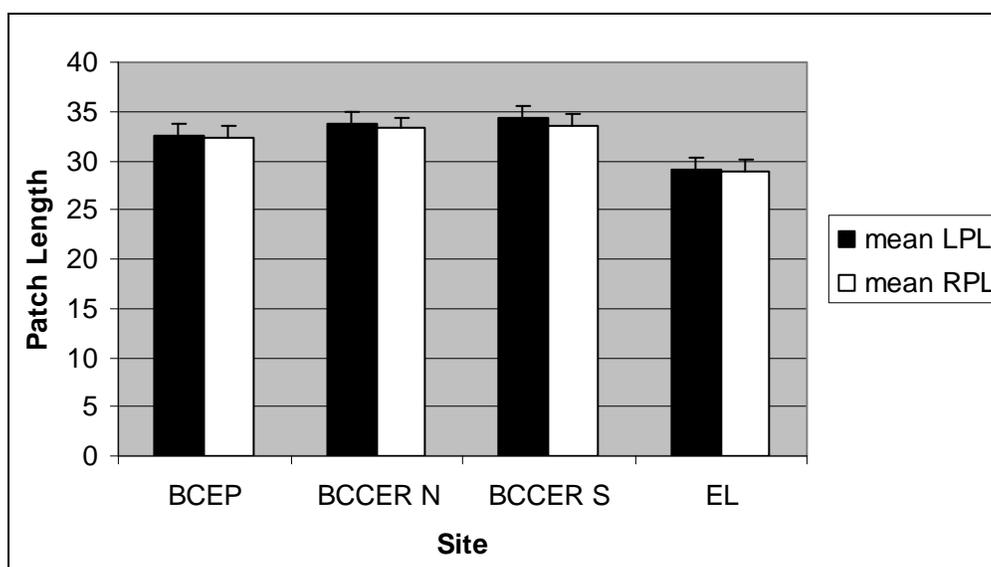


FIG. 17. Differences in mean patch lengths for male lizards between field sites. Standard error bars are included.

Length of abdominal patches in similarly sized males was not found to be significantly more asymmetric with greater patches in relation to SVL than those with smaller patches. Only a slight linear relationship with a correlation coefficient of $R^2=0.167$ was observed. Nevertheless, no strong linear relationship was found, thus predictions for abdominal patch asymmetry based on SVL could not be drawn (Figure 19).

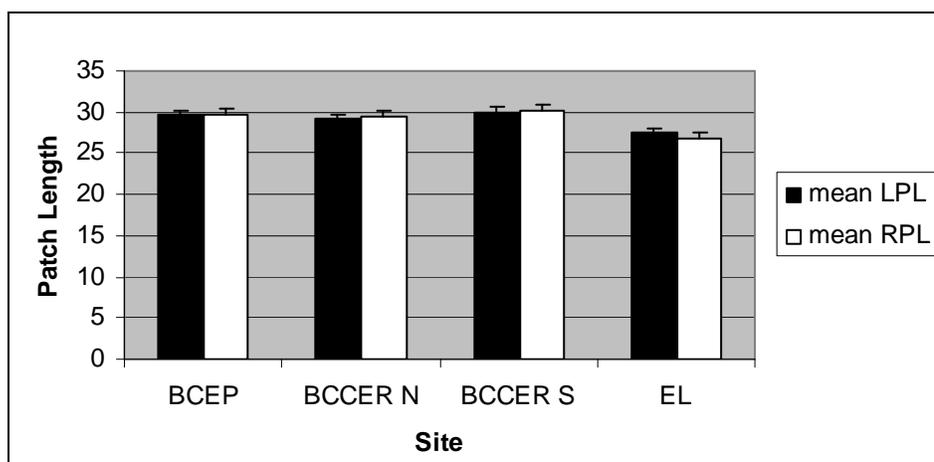


FIG. 18. Differences in mean patch lengths for female lizards between sites. Standard error bars are included.

TABLE 1. Summary of the type of bilateral asymmetry expressed in abdominal patches of male lizards between sites.

Site	Individuals Processed	DA (left)	Other type of Asymmetry	<i>p</i> -value
BCEP	28		X	0.224
BCCER N	21	X		0.103
BCCER S	13	X		0.016
ELFS	27		X	0.197

Femoral Pore Asymmetry

A one-tailed paired t-test was used to determine if the number of femoral pores was greater on the left hind limb than on the right for both sexes across all field sites. Females had significantly more femoral pores on the left hind limb at the 0.10 *alpha* level ($p=0.07$). Results for testing if femoral pore number was greater in the left hind limbs of males across all field sites were not significant ($p=0.97$) (Figure 20).

TABLE 2. Summary of the type of bilateral asymmetry expressed in abdominal patches of female lizards between sites.

Site	Individuals Processed	DA (left)	Other type of Asymmetry	<i>p</i> -value
BCEP	25		X	0.37
BCCER N	19		X	0.80
BCCER S	27		X	0.65
ELFS	13	X		0.13

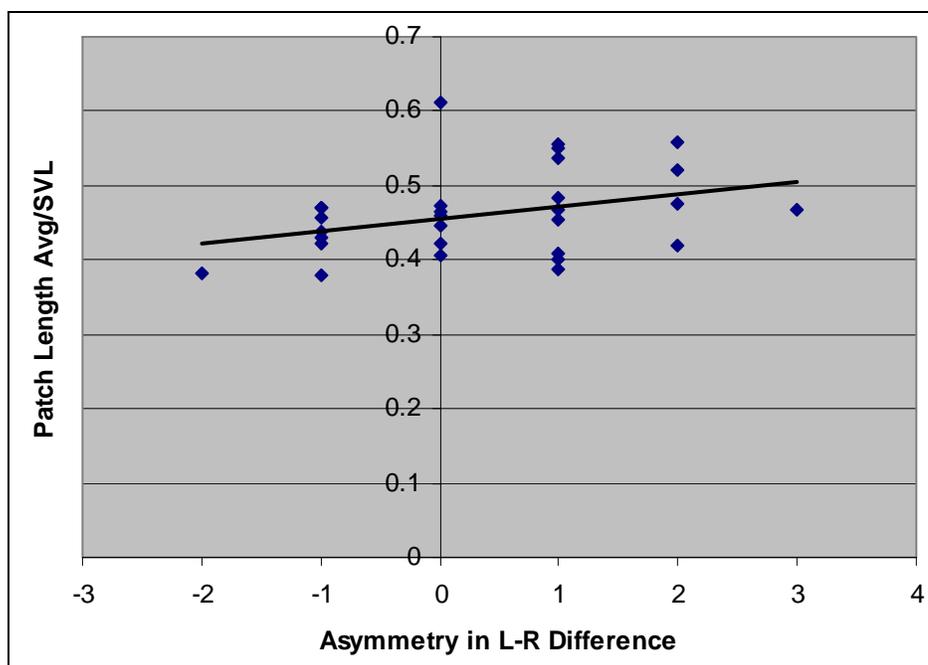


FIG. 19. Relationship between asymmetry in small to large patch length against SVL in similar sized adult male lizards (>65 to 72.5mm) among all field sites (BCEP, BCCER N, BCCER S, ELFS).

A one-way Analysis of Variance was used to determine if femoral pores were greater in number on the left hind limb than on the right for all lizards between field sites.

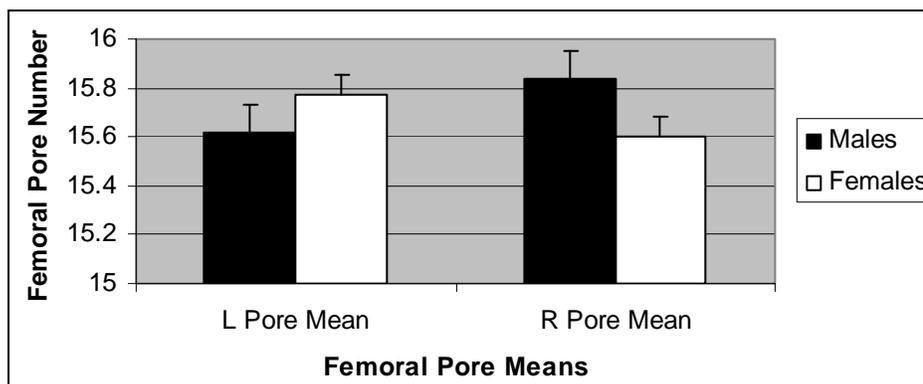


FIG. 20. Differences in mean values for femoral pores in lizards between sexes for all field sites (BCEP, BCCER N, BCCER S, ELFS). Standard error bars are included.

Lizards from the BCEP population showed a tendency ($p=0.107$). Lizards from the other three field sites showed no significant differences in femoral pore number (BCCER N: $p=0.81$; BCCER S: $p=0.2766$; $p=0.97$) (Figure 21).

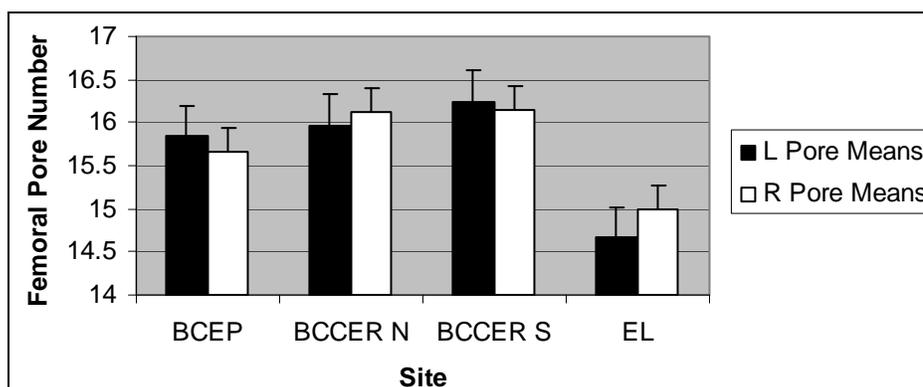


FIG. 21. Differences in mean values for femoral pores in all lizards between field sites (BCEP, BCCER N, BCCER S, ELFS). Standard error bars are included.

Males at BCEP had significantly more femoral pores on the left hind limb at the α 0.10 level ($p=0.07$). Males at the other three field sites were not found to show a greater number of femoral pores on the left hind limb (BCCER N: $p=0.998$; BCCER S:

$p=0.72$; ELFS: $p=0.991$). No significant differences were found for greater number of femoral pores on the left hind limb in females for populations at BCEP ($p=0.43$), BCCER S ($p=0.16$), or ELFS ($p=0.58$). However, there were significantly more femoral pores on the left hind limb in females at BCCER N ($p=0.02$) (Figures 22 and 23).

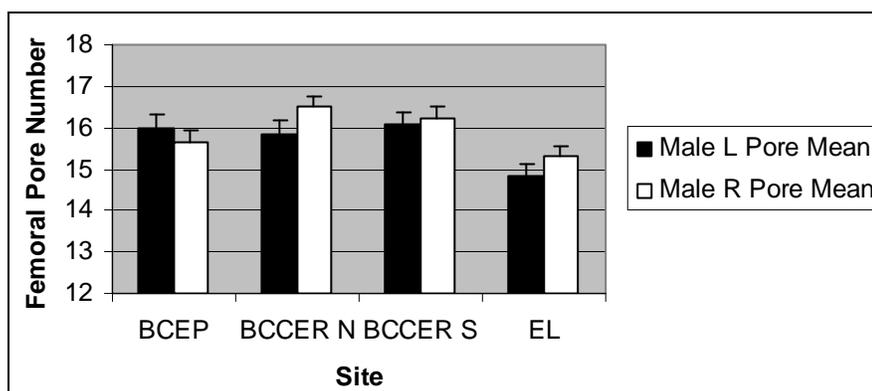


FIG. 22. Differences in mean values for femoral pores in male lizards between all field sites (BCEP, BCCER N, BCCER S, ELFS). Standard error bars included.

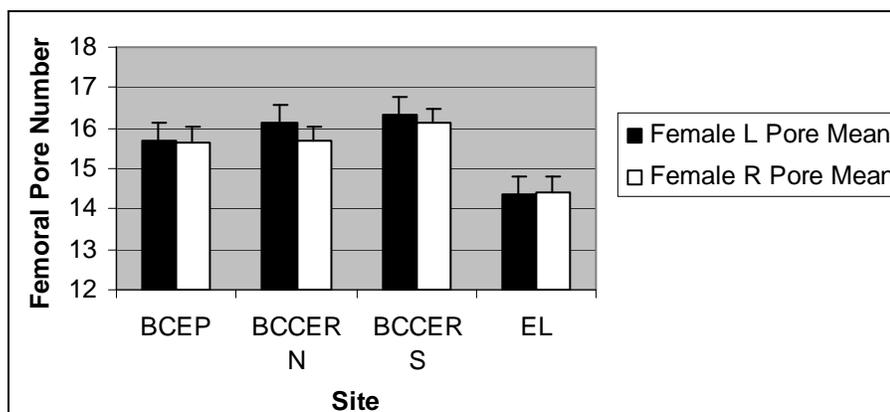


FIG. 23. Differences in mean values for femoral pores in female lizards between all field sites (BCEP, BCCER N, BCCER S, ELFS). Standard error bars included.

The number of femoral pores on the left hind limb was significantly greater than on the right for all lizards sampled from the Sutter Buttes ($p < 0.0001$) (Figure 24).

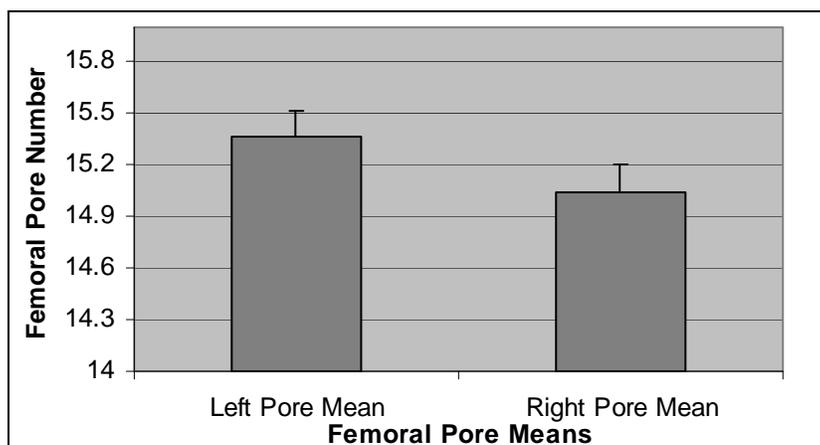


FIG. 24. Difference in mean values for left vs. right femoral pore number between all lizards ($N=100$ males, 100 females) sampled from Sutter Buttes. Standard error bars are included.

Further, femoral pore number on the left hind limb was significantly greater than on the right in both males ($p < 0.0001$) and females ($p = 0.01$) from the Sutter Buttes population (Figure 25, Tables 3 and 4).

There was no correlation found between number of pores on the left leg and length of left abdominal patch for either sex. No strong linear relationship was found for either males ($R^2 = 0.0329$) or females ($R^2 = 0.1860$).

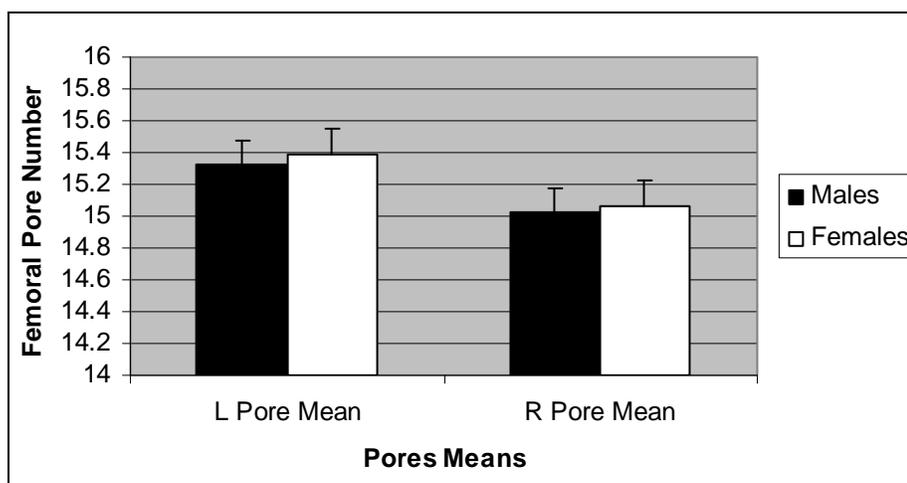


FIG. 25. Differences in mean values for femoral pores between sexes for Sutter Buttes ($N=100$ males, 100 females). Standard error bars are included.

TABLE 3. Summary of the type of bilateral asymmetry expressed in femoral pores of male lizards between sites.

Site	Individuals Processed	DA (left)	Other type of Asymmetry	p -value
BCEP	28	X		0.07
BCCER N	22		X	0.99
BCCER S	13		X	0.72
ELFS	27		X	0.99
Sutter Buttes	100	X		<0.0001

TABLE 4. Summary of the type of bilateral asymmetry expressed in femoral pores of female lizards between sites.

Site	Individuals Processed	DA (left)	Other type of Asymmetry	<i>p</i> -value
BCEP	26		X	0.43
BCCER N	19	X		0.02
BCCER S	27		X	0.16
ELFS	14		X	0.58
Sutter Buttes	100	X		0.01

CHAPTER IV

DISCUSSION

A number of questions were investigated regarding the significance bilaterally asymmetric secondary sexual characters may have in *Sceloporus occidentalis* social systems. It was predicted that abdominal patch length would be greater on the left side of the body in correlation to a preference for the use of the left visual field during agonistic encounters. It was also predicted that femoral pore count might be greater on the left hind limb than on the right in this species, as asymmetry is evident in this trait and chemical perception in lizards during aggressive interactions is not well understood.

Most studies on lateralized aggression have demonstrated this phenomenon only in males, however lateralized aggression recently showed a left eye preference in females of *Sceloporus virgatus* during female rejection displays towards males (Hews et al., 2004). Though a sister species to *S. occidentalis*, *S. virgatus* does not exhibit abdominal patches in either sex, a derived characteristic that has been lost in this species and others within this genus (Wiens, 1999). The patches used by male *S. occidentalis* during male-male agonistic displays were predicted in this study to set off mental cues to an opponent that the amount of blue within the patch might elicit more aggression from the left side of the body than the right and/or indicate fitness. Further, female iguanids do not typically exhibit aggression to the degree that males do (Sloan and Baird, 1999),

although females are known to at least display their abdominal patches towards courting males in order to express their unwillingness to mate.

It was suggested by Alvarez (1995) that the larger and more heavily adorned right antlers of fallow deer (*Dama dama*) may correlate with a preference to fight from the right side. Though left eye preference during intraspecific agonistic interactions appears to be consistent among tetrapods, the preference for the side of the body in such interactions may vary among taxa based on morphology and the signal or weapon used in combat. Because antlers are used as weapons and male deer battle head-on, they may position themselves so that the left eye is preferred visually but the right antler is preferred physically, as observed in the typical boxing stance in humans. In contrast to deer and humans, male lizards typically position themselves in a head-to-tail orientation during agonistic encounters, so that the left visual field is facing the left side of the opponent's body for either lizard.

Pélabon and Joly (2000) later demonstrated that the number of antler points in fallow deer increased with age and dominance did tend to increase with the number of antler points. However, no relationship between DA in antlers and dominance was found. Further, DA was found to be shifted to the left in antlers of the Alaskan moose (*Alces a. gigas*) (Bowyer et al., 2001). Whether this dissimilarity in DA is characteristic of these respective cervid species or a reflection of environmental factors relative to the specific populations in each study is unknown.

Graham et al. (1998) suggested that DA, FA, and antisymmetry are dynamically interrelated, being a part of a continuum rather than separate phenomena, and that transitions from one type of asymmetry to another are commonplace. A number

of studies have presented evidence in support of this suggestion. For example, Leary and Allendorf (1989) showed that antisymmetry was generated in the mandibular pores of rainbow trout (*Oncorhynchus mykiss*) under stressful conditions. Several passerine species of three populations in Kenya were shown to shift from FA to DA under high levels of forest fragmentation (Lens and Van Dongen, 2000). Further, Kark (2001) presented evidence that bilateral asymmetry in the length of the third toe in chukars (*Alectoris chukar*) can shift over populations within a geographical distribution as habitat type transitions from Mediterranean to ecotone to arid. These shifts in bilateral asymmetry have also been documented in invertebrates, including an Australian sheep blowfly (*Lucilia cuprina*) population, which shifted from FA to antisymmetry during the time taken to evolve resistance to Diazinon. The population then shifted back to FA once a resistance had been developed (McKenzie and Clarke, 1988). Additionally, fruit flies (*Drosophila melanogaster*) were found to exhibit DA in sternopleural bristles under the stress of high benzene concentration, while unstressed individuals exhibited FA (Graham et al., 1993).

In this study, asymmetries in the abdominal patches and femoral pores of *Sceloporus occidentalis* were measured at various localities in order to determine if DA was present and skewed to the left side of the body to correlate with left visual field use during agonistic displays. Since the same visual field (left being favored) is used by both individuals in agonistic encounters, it was suggested that the abdominal patch signal may also be larger on the left side eliciting more aggression from that side. Femoral pores are not known to be used in such encounters; however the prediction was made for this secondary sexual character, for the same (left) side of the body because asymmetry is

clearly present in this character. The functionality of femoral pores in lizard social systems is poorly understood; femoral pores might be used by *S. occidentalis* in a way yet to be understood. It appears that the type of bilateral asymmetry observed in *S. occidentalis* may be site-dependent, and while DA may be shifted to the left in one population, it may be shifted to the right in another. Contributing factors might include habitat, elevation, sympatry with the congeneric *S. graciosus*, or stress due to human encroachment and high levels of predation by species such as feral and domestic cats associated with such encroachment. There can be no clear conclusions drawn from this study regarding a correlation between femoral pores and left visual field preference.

Interestingly, BCEP was the field site where males deviated the most from left DA in abdominal patches. This site is the least pristine and most impacted of all field sites and it is possible that lizards in this population are examples of FA due to environmental stressors such as heightened predation pressures associated with human encroachment.

Measurements obtained from digital photographs for abdominal patch width and total surface area were not included due to the subjectivity of how the data were collected. Because the position of the sun and the shadow cast by each lizard was not taken into account during digital photography of the lizards, the number of entirely blue scales included for scale count measurements in Photoshop may not have been accurately represented at the exterior edge of the patch (especially the shaded left side of the lizard). This would affect both width and total surface area scale counts, but not length, for which only entirely blue scale rows were quantified for a length using the photographs in Photoshop. Further, the CD case cover used to keep the lizard venter on a level plain

during photography processing did not restrict limb or torso movement. While this did not have a negative effect on quantifying scales later, future studies might use more effective means of restraining lizards for other measurements involved with obtaining accurate abdominal patch length if taken out of hand. Scale counts used to determine patch length were predicted to be the most accurate method and yielded the most positive results. Additionally, collecting data for width and length using calipers was decidedly not an accurately effective method for these measurements due to the varied inner edges of the patch and how much the shape of the patch might change between breaths taken by the lizard (even though measurements were not taken until the lizard had exhaled and an effort was made to keep limbs parallel while being measured). Caliper data for patch length was collected as a comparative means for quantifying this trait, however, results indicated that this may not be the most effective method and thus were excluded.

Conclusions from this study include the following: 1) *S. occidentalis* collectively express left DA in abdominal patch length across all populations sampled, 2) males collectively express left DA in abdominal patch length across all populations sampled and females did not, 3) both males and females from the Sutter Buttes express left DA in the number of femoral pores on the left hind limb than on the right, 4) different patterns of bilateral asymmetry appear to be present among different populations in this species and thus, this phenomenon may indeed be more complex and dynamic than what has typically been represented in the literature. Many studies of bilateral asymmetry focus on a single population and assume that shifts of asymmetry within a given character are either rare or do not occur at all, offering the impression that a given character has a single fixed type of asymmetry (Kark, 2001). As observed in the results of this study,

bilateral asymmetry in two different characters (abdominal patches and femoral pores) in *S. occidentalis* were inconsistent among populations, regardless of methodology. The type of asymmetry observed may be reflected by the specific environmental effects present at the time and place a population is studied. Clearly, life history patterns and habitat use vary in widespread generalist species such as *S. occidentalis*. Further, some populations of *S. occidentalis* within this study are syntopic with *S. graciosus*, a species within the genus that also expresses blue abdominal and gular patches and exhibits similar display patterns. The populations sampled in this study range from 91 to 1558m, occurring in both Mediterranean and high elevation, semi-arid climates. Environmental factors are ever-changing forces contributing to constant fluctuations in the dynamics at population and community levels of a given ecosystem. Bilateral asymmetry observed for a species measured at one population at one point in time may only be the norm for that specific population and/or that time, and generalizations should not be made for what may be observed throughout the geographic distribution of that species. This should especially be noted for wide-ranging taxa.

This research suggests that a correlation may exist between the use of a bilaterally asymmetric morphological character (abdominal patches) and aggressive displays using them mediated by neurological asymmetry in *S. occidentalis*. This research also contributes to the evidence presented by such studies as Kark (2001) investigating a single trait of the chukar shown to shift over geographic distribution. But because this study was conducted during a single field season and individuals were only measured once, it cannot be determined if a shift in asymmetry over time is present in the traits measured within or between sexes and/or populations.

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