THE EFFECT OF TAIL LOSS ON SPRINT SPEED, MATING STRATEGIES, AND TERRITORY SIZE AND QUALITY IN THE LIZARD *UTA STANSBURIANA*

By

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CHAPTER I

The differential effect of tail autotomy on sprint performance between the sexes in the lizard *Uta stansburiana*

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ABSTRACT

Autotomy of an appendage, especially the tail in lizards, can aid in escape from predators, but it comes with associated costs. In previous studies, decreases in sprint performance often follow from tail loss in lizards. We measured the impact of tail autotomy on sprint performance in the lizard *Uta stansburiana,* a species with intense predation pressure and consequently frequent natural tail loss. Sprint performance was measured using both maximal sprint speed and average stride length. We examined the impacts separately for each sex, as this species is strongly molded by sexual selection and tail autotomy is known to affect the social status of subadult *U. stansburiana* differently. To first check for sexual differences in native sprint performance, we assessed both sexes with intact tails. Neither sprint speed nor stride length significantly differed between the sexes before tail autotomy. Following tail loss, male performance was not affected; individuals maintained their previous maximal sprint speed and average stride length.

However, females significantly decreased both maximal sprint speed and average stride length following tail autotomy. Males maintained sprint speed after tail loss (but not by an increase in stride length) and females decreased in both measures of performance. We suggest that tailless males compensate for tail loss and maintain performance for the benefit of high speeds used for repulsion of male rivals from their territories. Females may well adopt an alternate social role following tail autotomy and thus not require fast sprint speed to defend territories.

Autotomy of an appendage, especially the tail in lizards, can aid in escape from predators, but it comes with associated costs. In previous studies, decreases in sprint performance often followed tail loss in lizards, and potential sexual differences following tail autotomy can provide evidence for the possible influence of sexual selection on performance in lizards. We measured the impact of tail autotomy on sprint performance in the lizard *Uta stansburiana,* a species that has frequent natural tail loss. Sprint performance was measured using both maximal sprint speed and average stride length. We examined the impacts separately for each sex, as this species is strongly molded by sexual selection and tail autotomy is known to affect the social status of male and female subadult *U. stansburiana* differently. To check for sexual differences in sprint performance, we assessed both sexes with intact tails. Neither sprint speed nor stride length significantly differed between the sexes. Following tail loss, male performance was not affected; individuals maintained their previous maximal sprint speed and average stride length. However, females significantly decreased both maximal sprint speed and average stride length following tail autotomy. We suggest that tailless males maintain high speeds to escape predators because of greater conspicuousness due to sexual dimorphism and behavior, and for repulsion of rivals from their territories. Post-autotomy females may adopt an alternate social role that does not require their prior sprint speeds. Sexual selection may have advanced this sexually different response in sprint performance to tail autotomy.

Predation is an ecological interaction between species that has led to an incredibly diverse suite of responses and behavior on the part of both predator and prey (Vamosi, 2005). The obvious benefit of antipredatory adaptations of prey is escape from being eaten. However, there are concomitant costs. The expression of one defensive behavior may compromise the effectiveness of a different antipredatory behavior or have far-reaching costs on the organism's future performance of other activities (Langerhans, 2006). Like all adaptations, antipredator defenses take their final form as a compromise between costs and benefits.

Lizards are the prey of many organisms and in response have evolved complex antipredatory defenses, including crypsis, tonic immobility, fast escape, armor-plating or spiny scales, threat displays, biting, scratching, striking with the tail, venomous saliva, squirting blood from the eyes, and tail autotomy (Greene, 1988; Pianka and Vitt, 2003). The last of these is particularly interesting because it is such an extreme defense, which has clear physiological costs and sometimes social costs (Fox and Rostker, 1982; Fox et al., 1990: see Bateman and Fleming, 2009 for a recent review).

Tail autotomy is the active process of breaking away a portion of the tail in response to a predatory attempt (Arnold, 1984). Autotomy occurs along a predetermined fracture plane or weak joint in the tail vertebrae. The ability to lose the tail varies in lizards with many (such as members of *Uta*, *Plestiodon,* and *Lacerta)* having especially adapted traits to minimize the costs of losing a portion of the tail. These traits include aligned muscle septa separating not tearing, breaking the vertebrae only at fracture planes, and aligned sphincter valves in blood vessels to reduce blood loss (see Arnold, 1988 and Bateman and Fleming, 2009 for reviews). These anatomical and physiological traits facilitate ease of tail loss and reduce its immediate costs. Costs associated with tail autotomy in lizards include a reduction in sprint speed (Punzo, 1982; Daniels, 1983; Dial and Fitzpatrick, 1983; Chappelle et al., 2004, Goodman, 2006; Cooper et al., 2009; but see Brown et al.,1995 and McConnachie and Whiting, 2003), decreased home range size (Martín and Avery, 1996; 1998), lowered social status (Fox and Rostker, 1982, Martín and Salvador, 1993a), decreased attractiveness as mates for females (Langkilde et al., 2005), reduced access to mates (Martín and Salvador, 1993a; Salvador et al., 1995), compromised feeding behavior (Martín and Salvador, 1993b), loss of energetic stores (reviewed in Bernado and Agosta, 2005), reduced reproductive output (Dial and Fitzpatrick, 1983), increased flight initiation distance and use of refugees (Cooper, 2007; Cooper and Wilson, 2008), and decreased subsequent survivorship (Wilson, 1992; Fox and McCoy, 2000).

Our objective was to determine the impact of tail autotomy on the sprint performance of *Uta stansburiana,* especially focusing on any possible sexual difference since the social consequences of tail loss are different between the sexes in this species (Fox et al., 1990).

Therefore, we 1) first compared the sexes of *U. stansburiana* with intact tails for two measures of sprint performance (speed and stride length), 2) then determined the impacts of tail autotomy on sprint performance, and 3) contrasted the impacts of tail autotomy on the two sexes separately.

MATERIALS AND METHODS

Study animals

During October 15-17, 2007, we collected 76 subadult side-blotched lizards (*U. stansburiana*) from a site in Winkler Co., TX. We captured lizards with a V-shaped mesh trap (see Fox 1978 for description) or occasionally by hand. Following capture, we placed lizards in cloth bags and transported them in a cooled ice chest back to Oklahoma State University. We recorded snout-vent length (SVL), tail and total length, mass, and sex for each individual. As expected, the sexes were dimorphic; males were significantly longer than females for all measures of length and also significantly heavier (*t*-tests, all $P < 0.0001$). The sexes also were sexually dichromatic, with males being more brightly colored. Six lizards with regenerated or missing tails were excluded from the trials.

We placed the lizards separately into plastic cages (15 X 30 X 10 cm). Each cage had sand substrate, a refuge, and was lit from above using a combination of a 100-watt incandescent light bulb and a 40-watt fluorescent Vitalite©. Lighting created a thermal gradient along the length of the cage and lizards were able to actively thermoregulate. Lizards were given water via spray misting and fed a combination of crickets and mealworms *ad libitum* at least every other day.

Sprint trials

Following a 2-week acclimation period in the laboratory, we measured maximum sprint speed and average stride length. Lizards were induced to run along a 2-m sandpaper-lined track with a plexiglass side to allow video-recording. Each trial was recorded using two digital camcorders (Sony HandyCam DCR-SR42) in series. Both camcorders were placed 1-m away from and level with the track. The track had marked increments at 20-cm intervals to aid in reference during the video analysis. To induce maximum sprint speed an experimenter (CNC) stimulated the lizard to run by simulating a predator and chasing the lizard down the track with her hand. If a lizard stopped during a trial, it was tapped on the tail to spur it on. Each individual performed three sprints in a 12-h period, with at least 1 h of rest between trials. Prior to each trial, each individual was placed in a separate cloth bag and then into a lighted incubator set at 37° C for at least 1 h. We used the recordings of both camcorders to measure the fastest speed in any 20-cm segment per lizard. We calculated stride length indirectly by dividing distance sprinted by number of strides taken. For greatest precision, we counted the number of strides over the longest distance possible recorded by one camera in the trial producing the fastest speed. In most cases this was 50 cm; however, due to differences in video quality, for some trials we used shorter distances for this count.

The day following the trials, we induced autotomy of two-thirds of the tail to half of each sex by pinching the tail lightly with the thumb and forefinger (Fox and McCoy 2000). The proportion of the tail removed was not significantly different between males and females ($t_{68} = 1.388$, $P > 0.05$). The remaining lizards were handled in a similar manner with the exception that tail autotomy was not induced. Two weeks after the initial trials (Run 1), we again ran all lizards, both the autotomized and intact-tail groups, on the same track under the same conditions (Run 2).

Statistical analyses for normality and homogeneity of variances for each dependent variable (sprint speed, stride length, and differences in Run 2- Run 1 for sprint speed and stride length) were performed for each sex separately. The Kolmogorov-Smirnov test confirmed normality in all variables (all $P > 0.05$), except female sprint speed in Run 1 (K-S Z = 1.379, $P = 0.04$). A log transformation corrected this deviation from normality in females (K-S Z = 1.157, $P = 0.14$) and left the distributions for males normal (K-S Z = 0.842, $P = 0.48$). These log transformed sprint speeds were used in subsequent analyses. All dependent variables had homogeneous variances according to Levene's Test (all $P > 0.05$).

RESULTS

Sexual differences in sprint performance

Sprint Speed

During the pretreatment phase (Run 1), all lizards had intact tails and we compared native maximum sprint speed between males and females. Mean maximum sprint speed (mean ± 1 SD) for males was 1.756 ± 0.41 ms^{-1}, $n = 31$, and for females was 1.713 ± 0.36 ms^{-1}, $n = 39$. These speeds are slightly slower than those reported for adult *U. stansburiana* by Bonine and Garland (1999), but similar to those of Miles (1994).

To analyze the impact of sex on log maximum sprint speed, we performed ANCOVA with the covariate body size (SVL). The covariate SVL did not have a significant interaction with sex ($F_{1,66} = 0.269$, $P = 0.61$), so the interaction term was removed for the second step of the ANCOVA. Neither the covariate SVL nor the independent variable sex had a significant effect on log maximum sprint speed (Table 1), thus males and females did not run at significantly different speeds.

Stride Length

Mean stride length (mean ± 1 SD) for males was 47.26 ± 9.40 mm, $n = 26$, and for females, 46.92 ± 9.70 mm, $n = 35$. We used the same covariate, SVL, to compare stride length of the sexes. SVL did not have a significant interaction with sex (SVL*sex: $F_{1,57} = 0.068$, $P = 0.80$), so the interaction term was removed for the second step of the ANCOVA. SVL had a significant influence on average stride length (Table 1), but sex did not. Thus, average stride length was not significantly different between the sexes, correcting for differences in SVL.

Changes in sprint performance following tail autotomy

Sprint Speed

Because of the potential for body size to confound a comparison of change in sprint speed in relation to tail condition, we first tested for differences in SVL between treatment groups for each sex. SVL did not differ between control and treatment groups for males ($t_{29} = -0.401$, $P = 0.69$) or females ($t_{36} = -0.600$, $P = 0.55$), so it was not necessary to conduct ANCOVA with SVL as a covariate.

Using an independent-samples *t*-test, we found no significant difference in change in sprint speed between control and treatment male lizards ($t_{29} = -0.459$, $P = 0.65$; Figure 1a). Tail autotomy did not influence sprint speed in males. However, we did find a statistically significant decrease in sprint speed between control and treatment female lizards (t_{37} = -2.187, P = 0.034; Figure 1a). Therefore, female *U. stansburiana* had slower sprint speeds following tail autotomy.

Stride length

As a component of sprint performance, average stride length may also be impacted by the loss of a portion of the tail, especially since males somehow maintained their sprint speed after tail autotomy (analysis above). Like for sprint speed, we compared the change in average stride length (Run 2 - Run 1) for control and treatment lizards for each sex separately. The sample for analysis of stride length was a subset of the sample of analysis for sprint speed because we had to exclude some subjects due to poor video. As above for sprint speed, we tested to see if control and treatment lizards differed in the potentially confounding variable of SVL. SVL did not differ between control and treatment groups for males (t_{24} = 0.681, P = 0.50) or females (t_{33} = -0.600, P = 0.55), so it was not necessary to conduct ANCOVA with SVL as a covariate.

We found no significant difference in change in average stride length between control and treatment male lizards (t_{24} = -2.323, P = 0.54; Figure 1b). However, we did find a statistically significant decrease in average stride length in females following tail autotomy (t_{33} = -2.187, P = 0.03; Figure 1b). Therefore, we observed the same trend as in sprint speed, a sexual difference in the impact of tail autotomy on stride length in *U. stansburiana*. Female lizards after tail autotomy had shorter average strides, whereas males maintained their average stride length following tail autotomy compared to intact controls.

DISCUSSION

Behavioral responses to predation are incredibly diverse, but all have avoidance of death as their benefit. However, this benefit can come with costs. In the case of tail autotomy, individuals elude the predator, but suffer costs as a consequence (see Bateman and Fleming, 2009, for a recent review). In *U. stansburiana,* tail autotomy decreases social status (Fox and Rostker, 1982) and increases mortality (Wilson, 1992; Fox and McCoy, 2000). We documented a further cost: significant decreases in sprint performance following autotomy, but only in females, not males.

We suggest that males compensated for tail autotomy and maintained prior sprint speed while females did not due to two possible reasons. First, in general males may experience a greater risk of predation than females (Magnhagen, 1991; Zuk and Kolluru, 1998; Costantini et al., 2007). Males are more conspicuously colored (Stuart-Fox et al., 2003; Husak et al., 2006), larger, and in *U. stansburiana* tend to be active more frequently and over more hours of the day (Irwin, 1965; Tinkle, 1967), all of which could increase predation pressure. Our study population, in the southern part of the species' range, experiences intense predation pressure from multiple types and modes of predation (i.e. birds of prey, other lizards, venomous snakes; Parker and Pianka, 1975). The ability to sprint at maximum speed even after tail autotomy likely helps males avoid predation, especially since post-autotomy males are still larger than females, more brightly colored, and continuing to defend territories and court females.

A second reason for the different response to tail autotomy in males and females relates to the overriding importance of male mating success in this virtually annual, polygynous population of *U. stansburiana* subject to strong sexual selection; males must be fast to succeed (as shown for *Crotaphytus collaris* in Husak and Fox, 2006 and Husak et al. 2006), but females are virtually guaranteed to be mated, no matter if they are fast or slow. It has previously been suggested by Fox et al. (1990) and Fox and McCoy (2000) that female *U. stansburiana* may adopt a different social strategy subsequent to tail autotomy. Subadult females use the tail as a status badge and signal lowered status following tail loss. Females signal to other females that they have lost a portion of the tail and therefore make the best of a bad situation (Fox et al., 1990), possibly adopting a subordinate role and living in inferior habitat (Fox et al., 1981), decreasing social and territorial activities, fighting less, and devoting the resources and energy saved to growth or investment in future reproduction (Fox and McCoy, 2000). Thus, females subsequent to tail autotomy, because they adopt a different social strategy, may no longer need to defend their presumably inferior territories and therefore do not need to sprint as fast. We suggest that males do not have this option. Tailless males do not use the tail as a status-signaling badge and therefore continue to fight (Fox et al., 1990). To successfully attract females and mate with them in this polygynous species, males must defend high quality territories. Males must be able to run at top speed to intercept, intimidate, and escort out of their territory any potential intruder. Also, males must actively court females within their territory to gain mating opportunities; the ability to pursue and overtake females quickly is vital to male reproductive success. So tailless males continue to employ the same social strategy they did before autotomy, and rely on the same fast sprint speed. We maintain that the post-autotomy differences in sprint performance between males and females are a consequence of sexual selection, which is a potent selective pressure in *U. stansburiana* with respect to other qualities like body size and coloration, territory size, activity, aggressiveness, and use of the tail as a status-signaling badge.

Only two previous studies with lizards have examined the relationship of sprint performance and tail autotomy with respect to the sexes. Chapple and Swain (2002) found that male *Niveoscincus metallicus* skinks showed a significant decrease in sprint speed following tail autotomy, opposite to what we found, and that this effect lasted for 12 weeks. Females decreased sprint speed after tail autotomy, but regained performance over the next 4 weeks. A major difference between our results and those of Chappelle and Swain is that in their trials all the female subjects were pregnant, and in our study none were gravid. We chose subadult lizards as subjects to avoid differences due to reproductive burden of pregnancy in females. In *U. stansburiana* at this locality, subadults are both sexually dimorphic and territorial (Tinkle, 1967; Fox, 1983), so the sexually disparate need for speed to escape predators and to repel conspecific intruders is present even in subadults. In a second study, Cooper et al., (2009) showed that tail autotomy lowered sprint speed in males and previtellogenic females, but not vitellogenic females; these latter females were already impaired by the burden of increased mass from the developing eggs and so did not show further reduction in sprint speed following tail autotomy. Shine (2003) showed a similar difference between gravid and non-gravid female *Lampropholis guichenoti* following tail autotomy.

In our study, because males and females with tails (no previous tail autotomy) sprinted equally fast, it would suggest that males are under no more selection (i.e., due to predation) for this performance trait than females. However, it may be more complex than that. In collared lizards (*Crotaphytus collaris*), males likewise do not have the potential to sprint faster than females (Husak and Fox, 2006). Nevertheless, males use more of their maximum sprint potential when responding to an intraspecific, intrasexual, territorial interloper in the field than females do. Instead, females use more of their potential to escape predators. This same differential use of maximum sprint potential between the sexes may be found also in *U. stansburiana*, and we suggest that this would be a fruitful line of investigation.

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Table 1.1 Comparison of log maximum sprint speed and average stride length of male and female *Uta stansburiana* with intact tails (Run 1), using ANCOVA with covariate SVL.

Dependent Variable	Independent Variable	df[a]	*F* [a]	*P* [a]
Log maximum sprint speed	Sex	1,67	0.03	0.86
	SVL	1,67	1.74	0.19
Average stride length	Sex	1,58	1.72	0.20
	SVL	1,58	10.73	0.002

[a] Following removal of non-significant interaction term.

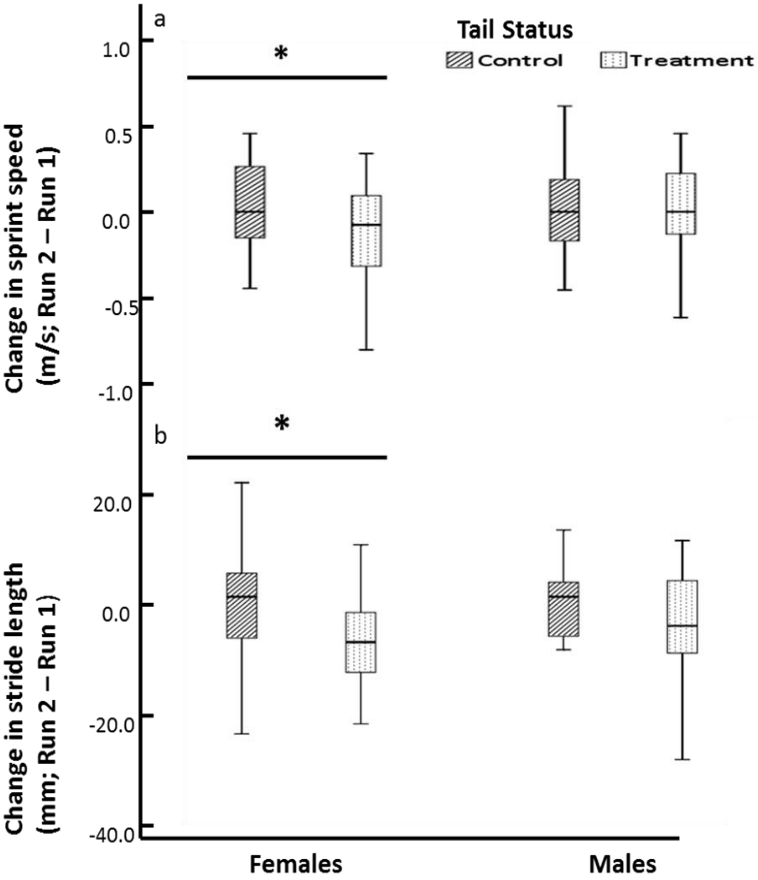

Figure 1.1 Comparison of changes in sprint performance between control and treatment (autotomy induced) groups in the lizard *Uta stansburiana*. (a) Changes in maximum sprint speed associated with tail status (b) Changes in average stride length associated with tail status. (* signifies significance at α = 0.05).

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CHAPTER II

A comparison of two methods to assess territorial aggression in the lizard *Uta stansburiana*

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ABSTRACT

Two methods, tethered-intruders and a mirror-image intruder, were employed to measure territorial aggression in the lizard *Uta stansburiana* in the wild. The use of a mirror in the field to assess territorial aggression is novel, and provided interesting results. This technique provides a new tool for herpetologists or behavioral ecologists interested in assessing territorial aggression or other aspects of social behavior in the field. The sexes responded with different amounts of total, weighted, and trial aggression to the two methods. Males were always more aggressive. Male aggression was not affected by tail status, as had been predicted; tailed and tailless males responded to intruders with similar aggression. However, the intensity and duration of the aggression towards the intruders of the two methods was significantly different in the males (regardless of tail status). Males responded to tethered intruders with significantly more total, weighted, and trial aggression than they did to their mirror-image. Females responded to the intruders of the two methods with equal amounts of aggression. Even though the mirror method did not elicit as much aggression and not all of the same aggressive behavior patterns as the real, tethered intruder, this method does have some obvious benefits. Both methods described

in this manuscript can be used to peek into the lives of lizards, and we recommend the use of both to elucidate different aspects of lizard territorial behavior.

Techniques to assess social behavior, and especially territorial aggression, are as diverse as the behaviors they measure. Aggression has been measured in response to many types of stimuli: conspecific tethered intruders, mirror images, video-playbacks, and even robotic models. These stimuli may be interpreted differently by males and females, individuals with differing social status or condition, different aged individuals, etc., and these groups of individuals may respond in disparate ways. Also, it is important to note that the methods commonly used in the laboratory may not yield comparable results in the field. We used two methods to assess territorial aggression in the lizard *Uta stansburiana*. Due to strong sexual differences in morphology and behavior and the known costs of tail autotomy on social status in *U. stansburiana*, we felt it would make an excellent organism to compare and contrast two field methods, and at the same time evaluate how autotomy impacts territorial aggression. Lizards, especially small territorial ones like *U. stansburiana*, are excellent models to study social behavior (Fox 1983; Fox et al. 2003). They are often abundant, easily captured, individually identifiable, and exhibit stereotypical complex behavior--all traits that make them ideal subjects for studies of social behavior. Lizard territoriality especially has been thoroughly studied (Stamps 1977; Fox 1983; Fox et al. 2003). In lizards, field studies often rely on two methods to quantify territorial behavior of residents: unmanipulated, time-constrained, focal observations (Baird et al. 1996; Baird et al. 2001) and experimental placement of tethered intruders into a resident's territory (Stamps 1977; 1978; Moore 1987; Fox and Baird 1992; Husak et al. 2006). Studies of dominance and territoriality in the laboratory use a different set of techniques, including dyadic contests in neutral arenas (Fox 1983; Fox et al. 1990; Husak et al. 2006; Karsten et al. 2009), mirror stimuli (Korzan et al. 2000; Brandt 2003; Brandt and Allen 2004; Hurd 2004; Watt et al. 2007), and video playbacks (Macedonia 1994; Clark et al. 1997; Ord et al. 2002). Mirrors work in laboratory settings to induce aggressive responses in lizards as well as in fish, birds, and primates (Gallup Jr. 1968; 1970; Bisazza and de Santi 2003; Moretz et al. 2007; Gouchie et al 2008; Hirschenhauser et al. 2008). The intensity and duration of lizard responses in the laboratory to a mirror have been used to measure endurance and aggression in lizards (Brandt 2003; Brandt and Allen 2004; Watt et al. 2007). However, the use of a mirror to induce an aggressive response from territorial lizards in nature has not previously been attempted. We took the mirror technique and transported it to the field to quantify territorial aggression. The tethered intruder method is a standard way to assess territoriality in the field. We compared the field-based standard of tethered intruder method to the typically laboratory-used mirror image intruder method, but here employed in the field.

We used the lizard *Uta stansburiana* for these tests because it is an abundant, territorial lizard with clear sexual differences in morphology and behavior and is easily observed with minimal disturbance. *Uta stansburiana* at our study site experiences frequent tail autotomy (Tinkle 1967; Fox and McCoy 2000), and in this population the tail is used by subadults as a social signal (Fox and Rostker 1982; Fox et al. 1990). The benefit of tail autotomy is escape from predation; however, numerous costs are incurred post-autotomy, including decreases in performance, loss of caudal resources, and altered social and territorial behavior (reviewed in Arnold, 1984 and Bateman and Fleming 2010). Therefore we also examined the impact of autotomy on territorial behavior.

The objectives of this study were to 1) compare the intensity and types of aggressive displays in the field against a mirror-reflected intruder versus a real, tethered intruder, and 2) evaluate differences in aggressive response due to sex and tail condition.

MATERIALS AND METHODS

The study was conducted at a site in Winkler County, Texas, located on a large cattle ranch and oil/natural gas field, from early March to late May 2009, the breeding season of *U. stansburiana* in western Texas. This site has been used for numerous studies examining the demography, life history, and behavioral ecology of *U. stansburiana* over the last 50 years (Tinkle 1962, 1967; Fox 1978; Fox and McCoy 2000; Anderson et al. 2012).

Method 1: Tethered Intruder. This method requires a size- and sex-matched intruder to be introduced into the territory of a resident lizard (Stamps 1977, 1978). Some residents had fully intact tails while others had autotomized tails in various stages of regeneration. For intruders, we used lizards collected from an offsite area of similar habitat. All intruders had fully intact tails. The intruders were kept in the laboratory in individual plastic cages and taken to the field only on the day of their trials. Intruders were provided with mealworms (*Tenebrio* sp.) *ad libitum* and their cage walls were misted with water each day. Intruders exhibited no signs of deterioration in condition due to captivity or manipulation, and were replaced with a new offsite lizard after several trials. Each intruder was paint marked with a single dorsal stripe (blue or red). Intruders were sorted into three categories: small, medium, and large (males: 42-45, 46-49, and 50-52 mm SVL, respectively; and females: 39-42, 43-46, and 47-50 mm SVL, respectively). Intruders were the same sex as the resident and matched in size as closely as possible. Each intruder was used at most twice a day, with the two trials separated by at least 4 hours. The intruder was secured (tethered) to a 3-m telescopic pole via a 10-cm segment of monofilament fishing line around its waist. Intruders were placed approximately 1 m from a targeted resident. The intruder's presence and/or behavior usually elicited a response from the resident; however, since the intruder was tethered, it could not chase the resident and never attacked it.

All trials were conducted by one investigator (LAW) and all behavior performed during a 10-minute trial was recorded. *Uta stansburiana* has very stereotypical territorial behavior, consisting mainly of headbobs, pushups, lateral displays, and circling, which have been observed and catalogued with relation to aggression in previous studies (see Table 1 modified from Fox 1983). Sometimes, aggression can escalate into a fight, with chasing and biting occurring. At this site, *U. stansburiana* seems largely unaffected by the presence of humans, often foraging or interacting with conspecifics within just a few feet of the observer. Trials were carried out during the morning (0900-1300) and then again in the late afternoon (1600-1930), corresponding with peak activity of *U. stansburiana* at the study site (Irwin 1965; Tinkle 1967; Anderson pers. obs.). Weather conditions were similar for all trials and an effort was made to avoid excessively hot or windy conditions.

Method 2: Mirror-Image Intruder. We custom designed a mirror for field use. The device consisted of a flat mirror (61 x 30.5 cm) mounted to a plywood board of similar dimensions. This board was connected to a 2-4 m collapsible pole. The pole was made of aluminum and lightweight, but rigid enough to support the weight of the mirror and board. This device was carried into the field and deployed once a resident lizard was located (Fig. 1). A different subset of resident lizards was used from those in Method 1. The mirror image was always size-, sex-, and condition- matched (including tail status) to the resident. The behavior of the intruder was also identical to the resident. So if the resident escalated its aggression, so did the intruder, and this cycle continued throughout the trial.

To deploy the mirror, the collapsible pole was extended to an appropriate length and the mirror was placed on the ground directly in the resident's line of sight. Due to the loose, sandy soil at the study site and the weight of the mirror/board, the mirror was easily placed at ground (lizard eye) level. If during this process the lizard fled from the experimenter, the trial was aborted and tried again later (> 5 hours).

Once the mirror was in place the trial began. All trials were observed by one investigator (LAW), and all behavior performed during the trial was recorded. Mirror trials were carried out during the morning (0900-1300) and late afternoon (1600-1930). Weather was similar for all trials, and again an effort was made to avoid excessively hot or windy conditions. Duration of the trials was dependent on the resident lizard. We tried to conduct 15-min trials, but in many cases had to cut the trial short because the intruder lost sight of the mirror image and left the area.

To account for the varying and different durations of the two methods, all frequencies of behavior patterns were converted to a common 10-min basis. Three dependent variables were calculated for each trial: total (raw) aggression, weighted aggression, and trial aggression. Total (raw) aggression is the sum of all agonistic behavior patterns observed during a trial; behavior patterns were categorically assigned a +1 if aggressive, and a -1 if submissive. The weighted aggression score is the sum of all agonistic behavior patterns observed during a trial, but each behavior pattern is given a weight from +3 to -1, based on the intensity of the behavior. See Table 1 for a detailed description, categorization of aggressive or submissive, and weights for each behavior pattern. Trial aggression was a single value based on the sequence of aggression observed during the trial; each trial was scored from zero to 5 (0=immediately flee, 1=no response, 2=display then flee, 3=display with no subsequent fight or flee, 4= display then fight, and 5=fight then display). Total Aggression and Weighted Aggression were log transformed to ensure normality, and in all cases in which parametric statistical tests were used, distributions of transformed data were normal (Kolmogorov-Smirnov tests, all $P > 0.05$). Non-parametric tests were used in the case of Trial Aggression since this was an ordinal, and not continuous, variable. All statistical comparisons were made using the statistical package SPSS (IBM Corp. Ver. 19.0).

RESULTS

During the spring of 2009, 48 tethered intruder and 33 mirror intruder trials were completed. Tethered intruders were introduced into the known territories of 20 male and 28 female lizards. The mirror was tested in the territories of 11 males and 22 females. Fewer males were tested because this population of *U. stansburiana* is female-biased, potentially due to differential predation pressure on the males. Males are more conspicuously colored, larger bodied, and defend larger territories, all of which may contribute to higher death rates due to predation (Magnhagen 1991; Stuart-Fox et al.

2003; Husak et al. 2006; Constantini et al. 2007). Size of the resident can affect aggressive response, but there was no significant difference in size of either male or female residents tested with the tethered intruder versus the mirror image (all $p > 0.05$, see Table 2 for details of morphological comparisons).

We first determined that *U. stansburiana* would act aggressively toward a mirror-image intruder in a natural setting. We observed an aggressive response from residents in 22 of 33 trials (67%). Of the 11 trials without aggression, in one the resident fled from the mirror and in 10 the resident showed no response. Comparing this to the introduction of real, tethered intruders, 29 intruders in 48 trials (60%) elicited aggression. We conclude that the mirror image of an individual *U. stansburiana* can elicit aggressive behavior from free-living, territorial resident lizards.

Within method analysis:

Tethered Intruders- Using a full-factorial two-way ANOVA, the interaction between the effects of sex and tail status on Total Aggressive response to a tethered intruder was non-significant ($F_{1,47} = 0.0010$, $P = 0.971$). Considering main effects, males were significantly more aggressive toward a tethered intruder than females ($F_{1,47} = 6.833$, $P = 0.013$; Fig. 2a), but there was no significant difference between tail status groups ($F_{1,47} = 0.970$, $P = 0.758$). When examining Weighted Aggression toward a tethered intruder, we found no significant interaction between sex and tail status ($F_{1, 37} = 0.001$, $P = 0.992$). Considering main effects, males were significantly more aggressive toward a tethered intruder than females ($F_{1,37} = 7.102$, $P = 0.012$; Fig. 2b) and there was no significant difference between tail status groups ($F_{1,37} = 0.058$, $P = 0.812$). Trial Aggression was assessed using the Mann-Whitney U Test. Males responded more aggressively against a tethered intruder than females (Mann-Whitney U = 109.0, $n_1 = 20$ $n_2 = 27$, $P < 0.0001$ two tailed; Fig. 2c). Tail status did not affect Trial Aggression for males (Mann–Whitney $U = 46$, $n_1 = n_2 = 10$, $P = 0.745$ two-tailed), or for females (Mann–Whitney $U = 60.0$, $n_1 = 11$ $n_2 = 16$, $P = 0.144$ two-tailed).

Mirror Image Intruders- No significant interaction between the effects of sex and tail status on Total Aggression toward a mirror image intruder was detected ($F_{1,\,22} = 0.008$, $P = 0.929$). Analysis of simple main effects showed that males were not more aggressive toward a mirror image intruder than females ($F_{1,22} = 1.074$, $P = 0.142$) and there was no significant difference between responses with respect to tail status ($F_{1,22} = 0.159$, $P = 0.564$). No significant interaction effect was detected between the effects of sex and tail status on Weighted Aggressive response to a mirror image intruder ($F_{1,\,26} = 0.032$, $P = 0.860$). Males tended to be more aggressive than females; however, this difference was not statistically significant ($F_{1,26} = 2.738$, $P = 0.111$). There was no significant difference with respect to tail status ($F_{1,24} = 0.301$, $P = 0.589$). Trial Aggression within mirror image intruder trials was assessed using the Mann-Whitney U Test. Trial Aggression was the same between male and female residents (Mann-Whitney U = 97.0, $n_1 = 11$ $n_2 = 22$, $P = 0.300$). Tail status did not affect Trial Aggression for males (Mann–Whitney $U = 14.5$, $n_1 = 6$ $n_2 = 5$, $P = 0.892$ two-tailed), nor females (Mann–Whitney $U = 46.0$, $n_1 = 12$ $n_2 = 10$, $P = 0.319$ two-tailed).

Between methods analysis:

To compare the two methods, we separated the sexes due to the sexual differences detected in the within method analysis. However, tail status was removed from the analysis; lizards with recent tail autotomy and those with intact tails were pooled.

Males responded to the two methods with significantly different amounts of Total Aggression ($F_{1,31} = 4.169$, $P = 0.050$; Fig. 3a). They responded with almost 1.5 times the mean aggressive behavior per 10-minute trial toward the tethered intruder than the mirror image intruder. Weighted Aggression from males toward the two types of intruders showed a similar tendency, but it was not statistically significant ($F_{1,31} = 3.681$, $P = 0.065$; Fig. 3b). Females did not show a difference in response to the two methods. Females responded with equal Total Aggression regardless of intruder type ($F_{1,32} = 1.070$, $P = 0.309$). Because variances of weighted aggression between the two methods were significantly non-homogenous for females, we used the nonparametric Mann-Whitney U-test to detect differences in Weighted Aggression to tethered intruders and mirror image intruders. The response of females was not significantly different (Mann-Whitney U = 270.0, $n_1 = 27$, $n_{22} = 22$, $P = 0.580$). Trial Aggression between tethered intruder and mirror image intruders was assessed by the Mann-Whitney U Test (tail status groups pooled). Trial Aggression of males against tethered and mirror intruders was significantly different (Mann–Whitney U = 60.5, $n_1 = 20$ $n_2 = 11$, $P = 0.022$ two-tailed; Fig. 3c). Trial Aggression of females was not different (Mann–Whitney U = 236.5, $n_1 = 27$ $n_2 = 22$, $P = 0.198$ two-tailed).

Additionally, we observed that residents (males more than females) presented with a real, tethered intruder not only scored higher quantitatively on indices of aggression, but they also behaved differently in a qualitative sense. Real intruders were attacked and ultimately bitten more. In 380 minutes of tethered intruder trials, 39 attacks and 27 bites were recorded, compared to only 5 attacks and no bites in 412 minutes of mirror trials. A major component of the stereotypical territorial encounter in *U.*

stansburiana is a phase of circling the intruder. In doing so, the resident dorsoventrally compresses its body, inflates its dewlap, and struts around the intruder in a tight circle. This behavior is a sign of escalating aggression and typically leads into a rough-and-tumble fight. During the 380 minutes of tethered intrusions, 31 instances of circling were recorded, as opposed to only 2 instances in 412 minutes of mirror intrusions.

DISCUSSION

The mirror successfully elicited territorial aggression in 67% of the trials. This was similar to the rate (60%) of eliciting territorial aggression toward a real, tethered intruder ($\chi^2 = 0.328$, df = 1, $P = 0.567$). However, the intensity and duration of the aggression against a tethered individual was noticeably different, especially in males. Residents attacked, and ultimately bit, real, tethered intruders more often than they tried to attack the mirror. The residents also used their full repertoire of territorial behavior against tethered intruders, including circling and lateral compression displays. These behavior patterns were much less frequently used against a mirror intruder. With the mirror technique, a resident cannot really circle the intruder, nor bite the plane of the mirror. In general, males responded significantly more aggressively than females toward a real, tethered intruder, but this sexual difference was not observed against a mirror image intruder.

Previous laboratory studies have shown decreases in social status for juvenile *Uta stansburiana* during neutral arena dyadic encounters following tail autotomy (Fox and Rostker 1982; Fox et al. 1990). We did not detect lower aggression from resident lizards with recent tail loss for any of the measures used in this field study. However, our methods differed significantly from those in the earlier studies, and the sudden appearance of an intruder (whether tethered or mirrored) into the territory of a resident may be impossible for tailless individuals to ignore. Our methods did not assess whether the resident would have won the encounter with the intruder, just its overall response. Perhaps the cost of territorial incursions by intruders is so high that residents must respond, regardless of tail status. Repeating laboratory dyadic encounters with adult lizards with and without tail loss is worth further investigation.

The use and limitations of tethered intruders to assess territoriality in the field have been discussed elsewhere (Fox and Baird 1992; Civantos 2000; Husak and Fox 2003; Husak 2004), so we focus instead on our novel use of the mirror intruder method deployed to assess territorial aggression in the field. Even though the mirror method did not elicit as high a level of aggression nor all the aggressive behavior patterns as the real, tethered intruder, this method does have some obvious benefits. The mirror projects an image of the intruder that is exactly matched to the resident with respect to size, sex, and condition. This is a major advantage because with the use of real, tethered intruders, care must be taken to ensure an appropriate match between resident and intruder, which is never perfect. Additionally, often small subsets of intruders are used, which can sometimes lead to deterioration in condition or motivation of the intruder and ultimately decreased aggression from the resident. The mirror image always “responds” in kind to the resident lizard’s behavior. This is not the case with a tethered intruder, who may or may not respond to the resident. This mirror response might show display endurance (Brandt 2003; Brandt and Allen 2004) and willingness or ability to escalate aggression (Cox et al. 2009) more reliably than a real intruder since the mirror image always responds aggressively to an aggressive resident.

In some studies the use of tethered intruders might not be practical or ethical. In cases where lizards are especially large (e.g., large iguanids or varanids) the tethering of an intruder seems impractical at best and may be dangerous to both investigator and the lizard. For threatened, uncommon, or endangered species, there may be legal or ethical concerns with tethering an intruder into the territory of a resident. Tethering, if done correctly, is a standard and safe method and does not cause long-term harm to the intruder. However, it may cause temporary stress to the tethered intruder because the intruder cannot flee and avoid the aggression of the resident, but it is unknown if this temporary stress is more than an unmanipulated, natural intruder experiences. In these cases, use of the mirror technique in the field might be a more suitable alternative.

The use of the mirror in a field setting does present some limitations. The most obvious limitation is the logistic demand of carrying a large, cumbersome mirror-on-a-pole into the field. The entire device weighed almost ten pounds, even with the modifications we made. For the pole, we used a lightweight aluminum pole used in swimming pool maintenance, and we constructed the backing board out of thin plywood. The placement of the mirror at our desert study site was made relatively easy due to the sparse vegetation and the sandy soil. Our method may not work in densely vegetated habitats or in rocky soils.

Another major limitation is lack of control of the stimulus of the mirror intruder. Basically, the resident loses focus on the intruder when the intruder passes out of sight. Unlike the tethered intruder technique (where the intruder is anchored to one small area), the mirror image may disappear during the trial when the resident moves too much to the side of the mirror. We observed this phenomenon, and we also sometimes witnessed the resident reach the edge of the mirror, lose the intruder, turn and walk back in front of the mirror. At this point the intruder "returns," and the resident begins its aggressive behavior again. To minimize this shortcoming, the size of the mirror must be appropriate for the size of the lizards. At our study site, adult *U. stansburiana* are approximately 48 mm in SVL, and the mirror was 610 mm in length, almost twelve times the lizard's body length. This size of the mirror allowed the resident ample opportunity to move while displaying, and never lose sight of the mirror image. For larger-bodied lizards, a larger mirror would be needed, but makes the device even heavier and more cumbersome.

The last limitation of the field mirror technique is that the deployment of the mirror can spook the resident lizard and cause it to flee. This occurred in a number of early trials, but, like with all techniques, with practice the investigator (LAW) became much more proficient at placing the mirror without disturbing the resident. The life-history and general behavior of *U. stansburiana* made this issue less troublesome than it might be with other species. *Uta stansburiana* are not nervous, or flighty, lizards. Residents occupy small territories and patrol often so as to prevent incursions from neighbors, and to switch ambush locations. So if residents are disturbed during the setup of the mirror, they often will return to this location within a short time and respond to their image, or allow the setup near their new location.

In sum, the mirror technique used in the field elicited aggression from residents but has limitations, as do all methods of eliciting aggression in a field study. The mirror results in aggression only if and when the resident is viewing its mirror image, and demonstrates only a certain level of aggression and not all aggressive behavior patterns. Real, tethered intruders clearly force the resident to engage in intense combative behavior, yet may give a false estimate of their social status since they cannot chase away the intruder. Both methods can be used to peek into the lives of lizards, and we recommend the use of both to elucidate different aspects of lizard territorial behavior.

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Table 2.1: Behavior patterns recorded and point values used to score total (raw) and weighted aggression.

Behavior	Type (aggressive or submissive)	Score	Weighted Score
Attack	Aggressive—resident runs toward and tussles with intruder	+1	3
Bite	Aggressive—resident bites intruder	+1	3
Superimposition	Aggressive—resident sets limb or body over intruder	+1	3
Lateral Display	Aggressive—resident extends limbs to raise the trunk of the body above the ground, while dorsoventrally compressing the torso and inflating the dewlap	+1	2
Pushup	Aggressive—resident performs rapid up and down movement in which the trunk of the body is raised off of the ground.	+1	2
Lick	Aggressive—resident licks intruder	+1	2
Circling	Aggressive—resident moves in a semi-circle or circle around intruder, often while performing other aggressive acts	+1	2
Headbob	Aggressive—resident performs up and down head movement without raising the trunk	+1	1
Approach	Aggressive—resident moves toward intruder	+1	1
Flee	Submissive—resident quickly and deliberately retreats from intruder	-1	-1
Flatten	Submissive—resident presses trunk of body and limbs flat against the ground	-1	-1

Table 2.2: Size (SVL) comparison between resident lizards challenged with a real, tethered intruder or the mirror-image intruder (*t*-tests).

Sex	Intruder Type	Sample Size	SVL (mm) ± 1 SD	*t*-statistic	df	*P* -value
Male	Mirror	12	50.83 ± 3.5	0.568	30	0.574
	Tethered	20	50.20 ± 2.29			
Female	Mirror	22	46.50 ± 1.82	1.184	48	0.242
	Tethered	28	44.21 ± 8.89			

Figure 2.1: The custom-designed mirror on a pole used to elicit territorial aggression. The pole is telescopic (2-4 m) and made of lightweight aluminum.

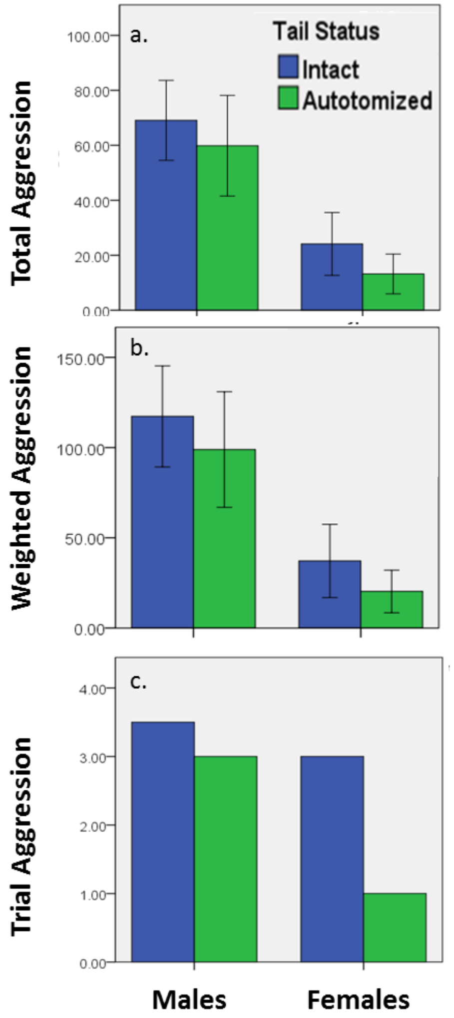

Fig. 2.2a: Total Aggression directed at a tethered intruder was significantly different for the sexes ($F_{1,47} = 6.833$, $P = 0.013$), but both sexes responded similarly regardless of tail status ($F_{1,47} = 0.0010$, $P = 0.971$). Error bars represent ±1 SE.

Fig. 2.2b: Weighted Aggression directed at a tethered intruder was significantly different for the sexes ($F_{1,37} = 7.102$, $P = 0.012$), but both sexes responded similarly regardless of tail status ($F_{1,37} = 0.001$, $P = 0.992$). Error bars represent ±1 SE.

Fig. 2.2c: Males responded with greater Trial Aggression than females when confronted with a tethered intruder ($U = 109.0$, $P < 0.001$), but both sexes responded similarly regardless of tail status.

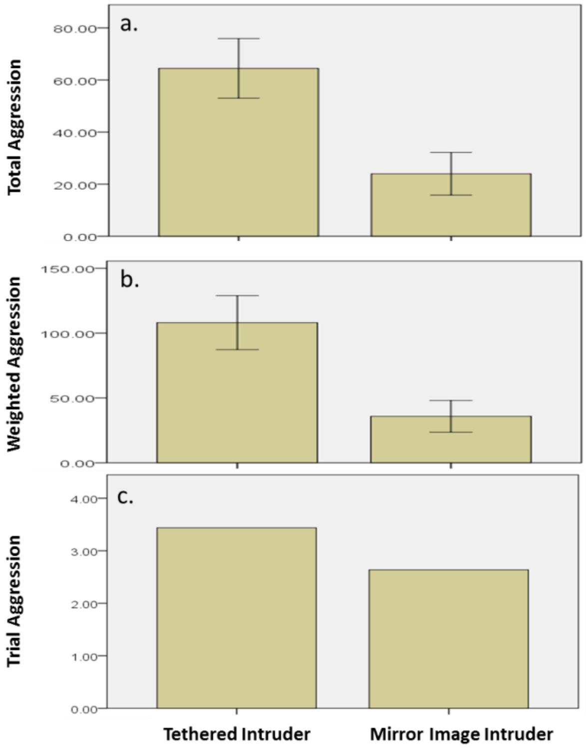

Fig. 2.3a: Total Aggression displayed by males in response to the two methods (tail status of males pooled). Males responded to the tethered intruder with significantly more Total Aggression than they did towards a mirror image intruder ($F_{1,31} = 4.169$, *P* = 0.050). Error bars represent ±1 SE.

Fig. 2.3b: Weighted Aggression displayed by males in response to the two methods (tail status of males pooled). Males responded to the tethered intruder with marginally more Weighted Aggression than they did towards a mirror image intruder ($F_{1,31} = 3.681$, *P* = 0.065). Error bars represent ±1 SE.

Fig. 2.3c: Trial Aggression displayed by males in response to the two methods (tail status of males pooled). Male responses to the tethered intruder were greater than their responses to a mirror image intruder (U = 60.5, *P* = 0.022).

CHAPTER III

Impacts of tail autotomy on territorial and foraging behavior in the lizard *Uta stansburiana*

ABSTRACT

Uta stansburiana in western Texas experiences intense predation pressure, and subsequently tail autotomy is common. Tail autotomy is an antipredatory tactic employed by lizards to avoid death by predation. Tail autotomy has been shown to be costly, e.g., reductions in social status, home range size or quality, and sprint performance, and in some species changes in mating and social strategies. We investigated the potentially negative impacts of tail autotomy on territorial and foraging behavior in *U. stansburiana*. We predicted that the impacts would be different between the sexes, as this species is strongly molded by sexual selection and previous work has shown sexual differences in behavior following autotomy. To measure territorial behavior, free-ranging lizards were tracked for a 20-min observation period in which all behavior was recorded. We observed differences in territorial behavior based on tail condition (fully intact, tailed versus recently autotomized, tailless individuals) and the sex of the individual. We also compared fecal production (used as a surrogate for food consumption) for a large subset of adult lizards with different tail condition. Tail status did not affect fecal output for either sex, even though tailless females foraged more frequently than their tailed counterparts. Post-autotomy strategies to cope with tail loss are different between the sexes. Tailless females forage more (but without increasing

fecal production) and fight less. Tailless males abandon territoriality and adopt a more cryptic, less assertive behavior, and become sneakers. These differences relate to the unique set of reproductive and sexual selective pressures facing each sex.

Tail, or caudal, autotomy is the active process of losing a portion of the tail to a would-be predator. In lizards, tail autotomy is common in many taxa (especially in skinks and iguanids); however, autotomy is completely absent in others (e.g., Chameleonidae and *Phrynosoma* horned lizards) (Zani 1996; Downes and Shine 2001). Tail autotomy comes with several co-evolved traits to minimize the immediate physical stress on the lizard (reviewed in Arnold 1984). The autotomization, or break, occurs only at pre-weakened fracture planes usually within the caudal vertebrae. The caudal muscles separate along septa at these fracture planes and do not tear during autotomy. Numerous sphincter valves in blood vessels are located near each fracture plane to prevent excessive bleeding at the autotomy site. Following autotomy, most lizards are capable of regenerating the tail, but this process is highly variable and carries its own set of costs (Ballinger and Tinkle 1979; Vitt 1981; Arnold 1988; McConnachie and Whiting 2003).

The obvious benefit of tail autotomy is escape from predation (Congdon et al. 1974; Daniels 1985; Arnold 1988). However, there are numerous costs associated with autotomy (reviewed in Arnold 1984; Bateman and Fleming 2009). Many lizards store lipids in the tail, therefore, the tail represents a major energetic investment (Dial and Fitzpatrick 1981; Daniels et al. 1986, Chapple and Swain 2002a; Chapple et al. 2002; Lin et al. 2006). Loss of this investment can lead to increased mortality (Wilson 1992; Fox and McCoy 2000), or lowered reproductive output (Dial and Fitzpatrick 1981; Wilson and Booth 1998; Chapple et al. 2002). Autotomy also significantly affects other antipredatory tactics (Cooper Jr. 2003; Cooper Jr. 2007). The tail plays an important role in balance and maneuverability in most lizards, and loss of the tail has been shown to decrease sprint performance in most lizards examined (Punzo 1982; Chapple et al. 2004, Goodman 2006; Cooper et al. 2009; Anderson et al. 2012), but there are examples where loss of the tail increased sprint speed (Daniels 1983; Brown et al. 1995; McConnachie and Whiting 2003). A decrease in sprint speed can lead to increased susceptibility to predation (Wilson 1992; Martín and Avery 1997; Niewiarowski et al. 1997; Fox and McCoy 2000) or an inability to successfully defend a territory (Martín and Salvador 1993b; Salvador et al. 1995; Webb 2006).

A less commonly explored consequence of tail autotomy is a potential decrease in the ability of tailless individuals [hereafter "tailless" means less than a full tail, not completely without a tail] to chase down and capture prey items (feeding success) due to decreased sprint speed or the potential relegation to suboptimal habitat where prey are less abundant (Martín and Salvador 1993a; Martín and Avery 1997). A decrease in sprint performance following autotomy would be doubly costly. First, the individual is slower and may be less successful at catching prey. Second, this lowered success rate comes at a time when the individual has lost its valuable store of energy (the tail) and when it needs more energy to regenerate the tail.

The costs of tail autotomy also include changes in social status and mating strategies. In *Uta stansburiana*, the side-blotched lizard, individuals who have lost their tails fall in social status (Fox and Rostker 1982; Fox et al. 1990). The change in tail status may force changes in social behavior. Tailless individuals, especially males in a polygynous breeding system, must continue to acquire and defend optimal territories. On the other hand, males that have lost their tails might abandon the strategy of territoriality and adopt an alternative reproductive tactic, like the sneaker strategy (Sinervo and Lively 1996; Oliviera et al. 2008). Yet these tailless individuals are handicapped due to the loss of energetic stores that were held within the tail and by any potential decrease in sprint speed. The handicaps associated with autotomy have been shown to lead to a decline in dominance (Fox et al. 1981; Fox and Rostker 1982; Fox et al. 1990; Martín and Salvador 1993a) and decreases in home range size and quality (Martín and Salvador 1993b; Salvador et al. 1995). Tailless individuals may also be challenged more by their tailed neighbors, leading to an increase in fighting and display behavior (Martín and Salvador 1993a). All these costs are magnified due to the depletion of energetic stores and the increased risk of predation associated with displaying and fighting. This increased predation risk additionally comes at a time when the tailless individual is missing its valuable anti-predatory tactic, tail autotomy.

In this study we followed individual lizards before and after tail autotomy to evaluate changes in social and mating behavior, and to measure feeding success of a set of these lizards with various degrees of tail loss. This species shows a decrease in sprint performance in females following autotomy (Anderson et al. 2012); decreased speed may lead to less prey captures, and therefore, lower feeding success. We measured fecal production (as a surrogate for food consumption) of tailed and tailless individuals to see if tail status affected food intake.

MATERIALS AND METHODS

The side-blotched lizard, *Uta stansburiana*, has a well-known life history, is abundant in appropriate habitat, and frequently employs tail autotomy to avoid predation. Its geographic range includes the western and southwestern United States and northern Mexico. Our study site was located within an active sand dune complex in Winkler Co., Texas. Dunes are constantly shifting and are sparsely vegetated. Lizards prefer the edges of the large dunes, where grasses and small shrubs act to stabilize the dunes. This population of *U. stansburiana* has been the subject of extensive research over the last fifty years, and therefore, its life history and demography at the site are well known (Tinkle 1967; Fox 1978; Fox 1983; Fox et al. 1981; Fox et al. 1990; Niewiarowski et al. 1997; Fox and McCoy 2000). *Uta stansburiana* is a small, insectivorous lizard (max. SVL = 58 mm). At this study site *U. stansburiana* is very short-lived, with less than 10% surviving to a second breeding season (Tinkle 1967; M. L. Anderson Pers. Obs.). It is an active ambush hunter, making rapid short-distance movements between ambush sites throughout the day. Both males and females actively defend the entire area within their home range, therefore the terms home range and territory are synonyms at this study site (Tinkle 1967). The small size and ecology of *U. stansburiana* make individuals highly susceptible to predation. There is intense predation from numerous predators, including snakes, birds, and other lizards (Tinkle 1967; Parker and Pianka 1975; Turner et al. 1982; Wilson 1992; Niewiarowski et al. 1997; Wilson and Cooke 2004). Tail loss is common; on average every lizard will lose its tail to a predator at least once in its life, and approximately 40% of the population at any given time is regenerating a portion of the tail (Tinkle 1967; M. L. Anderson Pers. Obs.). Previous work with *U. stansburiana* has shown that tail autotomy increases overwinter mortality (Fox and McCoy 2000), decreases social status and dominance (Fox and Rostker 1982; Fox et al. 1990), and recently it was found that autotomy leads to a decrease in female, but not male, sprint performance (Anderson et al. 2012).

Focal observations:

We conducted focal observations on a subset of lizards (2008 n = 36; 2009 n = 48) from a larger study. This subset contained both tailed and tailless (individuals with naturally or experimentally induced tail autotomy) lizards. Single individuals were followed for 20 minutes at a distance of 2-3 m with the aid of binoculars, and all behavior was dictated into a subcompact digital voice recorder. *Uta stansburiana* has a well-known and fairly simple behavioral repertoire (Table 1). As lizards move from one ambush site to another, they headbob periodically as they move, and these headbobs were the most frequently observed behavior. The lizards pushup or laterally compress their bodies only during encounters with conspecifics, and the males use shutter-bobbing only during encounters with females. Foraging is a major portion of the daily activity budget of side-blotched lizards; they move around a lot and dart out from cover after any potential meal. *Uta stansburiana* eats a wide variety of invertebrates (including ants, spiders, and small moths; Tinkle 1967). Due to the enhanced visibility in such a sparsely vegetated area and the behavior of the lizards, it was easy to observe feeding attempts and tasting of the ground by all lizards. Nevertheless, we could not reliably categorize feeding attempts as successful or not (many prey are very small ants), and no attempt to do so was made.

Frequencies of behavior patterns recorded during each focal observation were converted into a common per minute rate. These rates were then used to compare individuals. Discriminant functions analysis (DFA) was used to quantify and visualize differences in behavior employed by tailed and tailless males and females. DFA tests to see if the patterns of behavior are nonrandom with respect to known groups. All statistical analyses were completed using SPSS ver. 18.0 (IBM Corporation).

Fecal Output:

At the end of the breeding season in 2008, 2009, and 2012, adult lizards (n = 23, 21, and 50, respectively) were collected from the study site. Food consumption for each individual was estimated by measuring its fecal production. Avery (1971) showed that fecal production of *Lacerta vivipara* served as a simple but remarkably accurate measure of food consumption. This method was also used previously with *Uta stansburiana* to determine if food consumption affected survivorship (Fox 1978). In our study, lizards were collected in the morning and brought to the laboratory. Sex was recorded and lizards were measured using a ruler (±1 mm) for snout-to-vent length (SVL), tail length (TL), and tail break length (TBL, from cloaca to scar from previous tail autotomy). Mass was recorded using a spring Pesola scale (± 0.25 g). Males and females are sexually dimorphic for both color and size, and can further be distinguished by the presence of enlarged post-anal scales in the males. Detailed morphological data for each sex and tail status group are listed in Table 2. Lizards were then placed in individual plastic petri dishes (150-mm diameter) that had holes in their lids to allow air exchange, and held in a climate-controlled room (20-25° C) for 72 hours. Lizards were not fed, but were provided water daily. After 72 hours, all fecal pellets in the petri dishes were collected and placed into glass vials. We made sure to exclude the precipitated white uric acid, which is found at the pointed end of the fecal pellet. Uncapped glass vials were then placed in a vacuum desiccator (Nalgene Corp.), and allowed to desiccate for 72 hours. This removed all moisture from the pellets so that a dry mass could be obtained. The pellets were then weighed on a Mettler-Toledo balance (±0.01 mg). This process was repeated on a small subsample of lizards, but drying time was increased to 14 days to determine if dry mass changed following a longer time in the desiccator. There was no difference between the dry mass of pellets after 72 hours and 14 days in the desiccator (paired $t = 0.116$, df = 12, $p = 0.278$). Consequently, fecal mass following 72 hours of desiccating time was used for all samples. The ratio of tail length to SVL was calculated for each individual. Lizards with a ratio of 1.5 or greater were classified as tailed (all had full intact tails) and lizards with ratios less than 1.5 were classified as tailless (all had a visible tail break; some had regenerating but not completely regenerated tails, and some had very recent tail breaks). ANCOVAs using lizard SVL as a covariate were used to compare the fecal production of lizards and determine if tail status affected fecal production, our surrogate for feeding success. Sexes were compared separately. All analyses were performed in SPSS ver. 18.0 (IBM Corporation).

RESULTS

Focal observations:

In the discriminant functions analysis of all four groups of lizards (tailed male, tailless male, tailed female, and tailless female), the first two functions explained a combined 97.3% of the variance. The eigenvalues of function 1 and 2 were 0.483 and 0.123, respectively, and canonical correlations for dimensions 1 and 2 were 0.571 and 0.331, respectively. The first function explained 77.5% of the variance, and the second function explained a further 19.8% of the variance among the four groups. The two functions showed a significant difference in patterns of behavior among the groups ($\chi^2 = 38.2$, df = 21, $p = 0.012$).

Function 1 was dominated by high values of headbobs and assertive behavior, and low values of other behavior (Table 3). Function 2 was dominated by high values of pushup displays and low values of prey capture attempts (Table 3). Complete lists of the standardized canonical discriminant function coefficients for both functions are found in Table 3. The values of the group centroids along each axis are provided in Table 4.

Function 1 corresponds to the horizontal axis and represents a continuum between performing the common and relatively metabolically cheap headbob displays and other assertive behavior versus the more costly and often agonistic other behaviors. Males, both tailed and tailless, were aligned along this axis (Figure 1 and Table 4). Tailed males tended to use headbobs and assertive behavior often, advertising their presence to neighboring males and females every time they moved. These males with full tails acted as would be predicted for a territorial male. Tailless males, however, performed less of these headbobs and assertive behavior and their scores were essentially centered around zero on axis one (Fig. 1 and Table 4). Their behavior seems to be one of little activity and avoidance of agonistic encounters; they did not behave like the tailed males. Tailless males were inconspicuous, even avoiding frequent headbobbing, which is typical of this species especially after a change in position from one place to another.

Function 2 corresponds to the vertical axis, and prey capture attempts and pushups (agonistic in nature and costly) anchored the positive and negative ends of this axis, respectively. Females were distributed along this axis, with both female group centroids aligning along it (Figure 2 and Table 4). Tailless females, compared to their tailed counterparts, spent more of their time and effort attempting to catch prey and rarely performed pushup displays, while tailed females foraged less and delivered pushups more frequently.

Fecal production:

The effect of tail status on total fecal output was compared against lizard size (SVL) using full-factorial analysis of covariance (ANCOVA). Sexes were separated for analysis. In males, the interaction of tail condition and the covariate SVL was not significant ($F_{1,33} = 0.190$, $p = 0.664$), so this term was removed from the model. In the reduced model, male fecal production was not significantly affected by tail condition ($F_{1,34} = 0.536$, $p = 0.469$) nor SVL ($F_{1,34} = 0.434$, $p = 0.514$). Tailless males apparently had similar feeding success as their tailed counterparts, regardless of SVL.

Like in males, the interaction of tail condition and the covariate SVL was not significant in females ($F_{1,53} = 0.242$, $p = 0.625$), so this term was removed from the model. In the reduced model, neither tail condition ($F_{1,54} = 0.865$, $p = 0.357$) nor SVL ($F_{1,54} = 2.323$, $p = 0.141$) significantly affected fecal production. Tailless females produced similar amounts of feces, therefore, ingested similar amounts of food, as their tailed counterparts, even though they attempted to feed more often as demonstrated by Function 2 in the DFA of behavior (Fig. 2).

DISCUSSION

Tail autotomy affects the behavior of breeding season adult *U. stansburiana* in a natural setting, and this altered behavior depends on the sex of the individual. Aligned with clear sexual differences in size, coloration, behavior, and diet in this species, each sex has developed unique strategies to overcome the costs of tail autotomy.

In males, tail autotomy leads to a decrease in assertive and headbobbing behavior, but not a change in feeding attempts or pushups. Tailless males avoid activities which may draw the attention of neighboring males. On the one hand, this strategy might allow them to maintain their territory without fighting as often, and without a tail, would probably lose these fights more often anyway (Fox and Rostker 1982; Fox et al. 1990). On the other hand, and more strongly suggested by the data, is that males who have autotomized their tails are adopting a conditional Alternative Reproductive Tactic (Sinervo and Lively 1996; Oliveira et al. 2008), that of a sneaker strategy, as suggested previously by Fox and McCoy (2000) for tailless males. If these sneakers can maintain fitness equal to their tailed counterparts, or even recoup some fitness as best of a bad situation, this would be a worthwhile strategy (Gross 1982; Nakashima 1987; Kempenaers 1995). Such tailless sneaker males would advertise less often, and provoke less agonistic encounters with neighboring males, while still seeking copulations with females. Tailless *U. stansburiana* males are known to respond aggressively when confronted by a tethered conspecific male (Anderson et al. 2013), but we do not know if this is true in all territorial interactions. One would expect fewer fights by tailless males if they are sneakers, but we did not observe less fighting in tailless males during our focal trials (but outright fighting was quite infrequent). It seems that tailless males try to avoid confrontation by performing less headbobs and assertive behavior (they are less conspicuous), but will fight back if approached too closely by a conspecific male. An interesting future avenue of investigation would be to see if tailless males in nature lose whatever fights they are drawn into more often than tailed counterparts, as laboratory experiments suggest (Fox and Rostker 1982; Fox et al. 1990).

In another lizard species, tail autotomy led to smaller home ranges (Salvador et al. 1995), and there was no evidence to suggest that males adopted a sneaker strategy following tail autotomy. We predict the opposite will happen in *U. stansburiana*: the tailless males, resorting to a sneaker strategy and seeking out unguarded females, will end up with larger home ranges than their tailed counterparts. In *U. stansburiana*, territory defense is important for male success and tailed males employ assertive and headbobbing behaviors to advertise their presence on territories without having to escalate to fighting. Following tail loss, males do not behave the same way, they become less conspicuous, move around more, and advertise less (i.e., sneaker males), but will fight if forced by a conspecific (rarely observed in this study) or challenged by an experimental intruder (Anderson et al. 2013).

Male fecal production was not affected by tail status. Apparently, tailless males fed as much as their tailed counterparts. The impact of tail autotomy on feeding behavior in males may be minimal, and so males continue to feed at the same rate regardless of tail status. The energetic needs of tailed and tailless males may be so similar that feeding is unaffected by tail loss. Or, as is the case in other species (Rose 1981; Merker and Nagy 1984; Deutsch et al. 1990; Durtsche 1992; Marler et al. 1995), territory defense is so important in males that feeding is neglected by males during the breeding season. The same may be true for tailless sneaker males attempting to find and mate with unguarded females. *Uta stansburiana* is virtually an annual lizard at this site, and the adult males used in the fecal production phase of the study had a very short life expectancy at this point in the season. Food intake may relinquish to territorial defense and mate searching regardless of tail status in males.

In females, tail autotomy leads to more foraging and less pushups. Unlike headbobs, pushups are directed only at a conspecific. We propose that tailless adult females signal lower social status, as tailless juvenile females did in the laboratory (Fox and Rostker 1982; Fox et al. 1990), and therefore, need to pushup less. So a decrease in pushups can be interpreted as a less aggressive strategy. Tailless females can accept (by signaling to other females) suboptimal home ranges, but will still garner copulations. Tailless females must attempt to feed more often on these suboptimal home ranges (and they did) to maintain growth equal to tailed counterparts, while also regenerating the tail (and producing clutches and eggs as large as those of tailed females) as observed by Fox and McCoy (2000).

Our focal observations showed that tailless females had more feeding attempts than their tailed counterparts. From this, it would be predicted that tailless females should feed more and produce more feces than their tailed counterparts, but this was not the case. However, our study did not examine whether they were as efficient at capturing prey as tailed females, or just spent more time foraging. The focal observations indicate the latter. So it might be that tailless females accept residency in suboptimal habitat, signal their lower social status from absence of the tail, fight less, and forage more just to take in as much food as tailed females. However, they allocate energy into tail regeneration as well as growth and reproduction and because they allocate less to fighting and territory defense, they can both regenerate the tail and grow and reproduce as much as tailed females (Fox and McCoy 2000). The energy they save from reduced fighting goes into tail regeneration and they feed equivalently to tailed females, although they have to have more feeding attempts in their suboptimal habitat. It is also of note that only female *U. stansburiana*, not males, decrease their sprint performance after tail autotomy (Anderson et al. 2012). This slower sprinting may affect their ability to successfully capture prey, in addition to foraging in suboptimal habitat. So they engage in more feeding attempts just to gather as much food as tailed females in better habitat.

Tail autotomy affects both male and female *U. stansburiana*. However, compensatory strategies to cope with the costs of autotomy are very different for the two sexes. Tailless females forage more and fight less, and signal their lower social status from the loss of the tail. Tailless males adopt a more cryptic, less assertive behavior, and become sneakers. These differences relate to the unique set of reproductive and sexual selective pressures facing each sex.

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Table 3.1: Description of behavior patterns observed during focal observations.

Behavior	Description
Aggressive (leading to contact)	Agonistic behavior directed toward a conspecific (including approaches, circling, lateral displays, superimpositions, and attacks or biting)
Pushups	Agonistic behavior directed toward a conspecific; (stereotypical up-and-down elevations of the body via flexure of the legs), but does not immediately result in contact
Submissive	Agonistic behavior signaling subordination (including flattening of the body and fleeing)
Assertive	Behavior important for territory maintenance but not leading to physical contact (including tasting and licking the ground, circumductions, and tail-twitching)
Headbobs	Most frequent behavior (stereotypical up-and-down movements of the head), used primarily following movements and during interactions with conspecifics
Movements	Short distance speedy movements to a new ambush site (often followed by headbobs)
Prey capture attempt	Movement from ambush site to attempt to capture a prey item

Table 3.2: Morphological comparison of tailed and tailless lizards used in fecal production analyses (means).

Sex	Tail Status	Sample size (n)	SVL (mm)	SVL (SE)	TL (mm)	TL (SE)	Tail to SVL ratio	Ratio (SE)	Mass (g)	Mass (SE)	Fecal Mass (g)	Fecal Mass (SE)
Male	Tailed	21	51.62	0.54	89.00	1.71	1.72	0.03	4.61	0.16	0.037	0.005
	Tailless	16	49.69	0.70	43.63	6.59	0.87	0.13	3.71	0.16	0.040	0.005
Female	Tailed	28	46.50	0.33	77.82	0.95	1.67	0.02	3.29	0.10	0.033	0.003
	Tailless	29	46.00	0.37	47.93	1.66	1.05	0.04	3.13	0.08	0.030	0.002

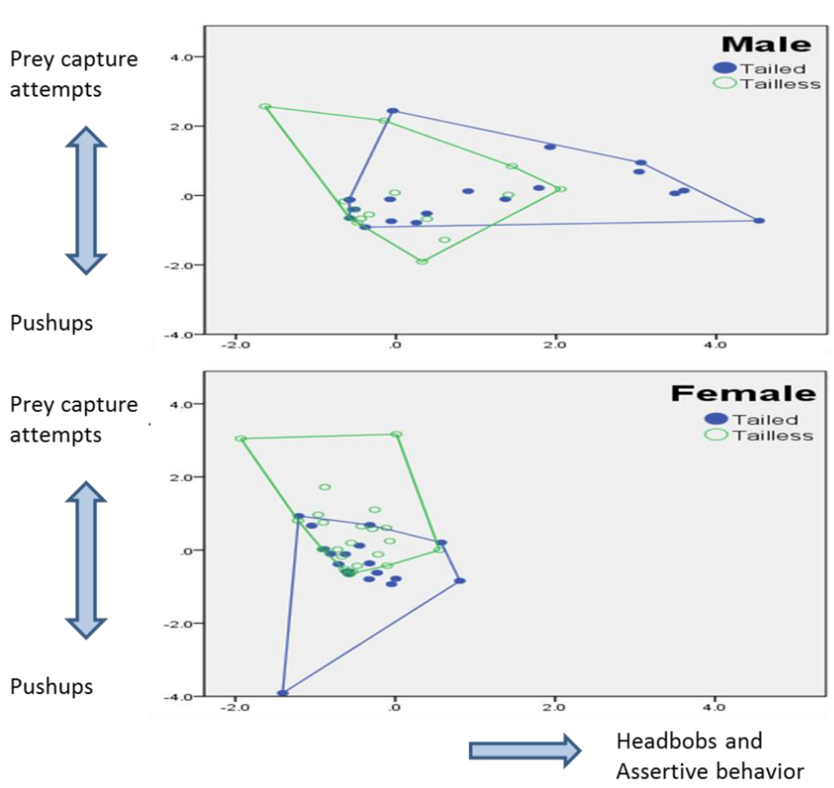
Table 3.3: DFA loading coefficients from analysis of behavior of the four sex and tail status groups.

Behavioral categories	Standardized Canonical Discriminant Function Coefficients	
	Function 1	Function 2
Aggressive	0.217	0.409
Pushups	-0.332	-0.787
Headbobs	1.028	-0.090
Submissive	-0.150	0.352
Assertive	0.440	-0.586
Movements	-0.210	0.425
Prey Captures	-0.290	0.705

Table 3.4: Values at centroids for each group. Greatest absolute difference in value shows greatest separation along a single function (axis).

Sex	Tail Status	Function	
		1	2
Males	Tailed	1.133	0.044
	Tailless	0.094	-0.081
Females	Tailed	-0.478	-0.451
	Tailless	-0.540	0.448

Figure 3.1: DFA results showing 100% minimum convex polygons surrounding tailed and tailless groups in a single analysis for males and females together.



CHAPTER IV

Impacts of tail autotomy on measures of territory quality and territorial behavior in the lizard *Uta stansburiana*

ABSTRACT

Tail autotomy in lizards can aid in escape from predators, but it comes with associated costs. In previous studies, decreases in territory size and overlap with conspecifics, plus decreases in movement followed tail loss in lizards. We measured territory quality (based on measures of size, overlap with other neighboring territories, and microhabitat diversity) and movements in the lizard *Uta stansburiana*. Predictions relating the impact of autotomy on survivorship, territory quality, average distance moved between sightings, and average days between sightings were made and tested. Geo-referenced sightings for each individual were taken in the field and then used to infer the territory boundaries. We examined the impacts separately for each sex; autotomy affects the sexes of *U. stansburiana* differently. To measure changes in territory quality we assessed two groups of lizards (control [tailed] and treatment [tailless]). The control and treatment groups did not differ in measures of territory quality or movements during the initial phase when all lizards had intact tails. Tail loss significantly decreased survivorship in both sexes. Control males maintained smaller territories, with fewer overlaps with neighbors, and increased microhabitat diversity over time. Territories of treatment lizards changed in opposite ways. Treatment males maintained larger territories, with the same number of overlaps with neighbors, and decreased microhabitat diversity over time. Territories of females did not change

differentially with respect to tail condition in size or overlaps, but the territories of tailed females decreased in microhabitat diversity while those of tailless females did not. Tailless males moved more than tailed males, while the mean days between sightings decreased for treatment and control males and females. Differences in the response to tail autotomy between the sexes are likely due to different costs and benefits for each sex. Tailless females use the tail as a status badge, and make the best of a bad situation. They defend lower quality, suboptimal territories. This leads to less fighting, and tailless females maintain their original territory size and number of overlaps with neighbors. Males do not have this option, and, as long as they retain their tails, must fight to defend large, diverse territories to attract females and protect them from intruding males. However, without a tail, males are at a disadvantage and lose more fights. These tailless males abandon territoriality and assume an alternate reproductive tactic, that of sneaker.

We examined territoriality in a population of the side-blotched lizard, *Uta stansburiana,* and tested predictions over the impact of tail autotomy on territory quality (based on measures of size, overlap with neighbors, and microhabitat diversity) during the breeding season. Additionally, we compared the effect of tail condition on the probability of survival, average distance moved between sightings, and mean days between observations for each individual during the breeding season. Prior studies have suggested a link between tail status and alternate reproductive tactics in this population of *Uta stansburiana* (Fox and McCoy 2000, Anderson et al. 2012). Disparate shifts in the behavioral tactics for the sexes are predicted; tailless males are predicted to assume a sneaker strategy to avoid conflict with tailed males, and tailless females, are predicted to signal lowered social status and accept suboptimal home ranges after tail autotomy (Fox and Rostker 1982; Fox et al. 1990). The shift from territorial male to sneaker male is predicted as tailless males (with lowered social status) attempt to maintain their fitness, but are less equipped for territorial defense than their tailed counterparts. The disadvantages to tailless lizards include reduced size, sprint performance and endurance (Mártin and Avery 1998; Chapple and Swain 2002; Anderson et al. 2012; but see Daniels 1985; Brown et al. 1995), decreased attractiveness (Mártin and Salvador 1993; Langkilde et al. 2005), lower growth rate (Ballinger and Tinkle 1979; Smith 1996; Niewiarowski et al. 1997; Goodman 2006), inability to perform courtship displays or alterations to displays (Salvador et al. 1995; Langkilde et al. 2005), lower social status (Fox and Rostker 1982; Fox et al. 1990), and modifications to foraging or basking behavior (Mártin and Salvador 1997; Cooper Jr. 2003). To examine the impacts of autotomy on the spatial behavior and territorial characteristics in *U. stansburiana*, the following predictions were developed and tested:

Prediction 1: Survivorship

Tail autotomy has been shown to reduce survivorship in *Uta stansburiana* (Wilson 1992; Fox and McCoy 2000). Reduced survivorship may occur for a number of reasons: tailless individuals (hereafter "tailless" means less than a full tail, not completely without a tail) have less energy stores, they run slower, and they are missing the tail to confuse subsequent predators or to escape via autotomy. We examined the impact of a significant loss of a portion of the tail during the breeding season on the probability of survival for resident adult *Uta stansburiana*. The prediction is that tailless individuals experience higher levels of mortality than tailed lizards and that this heightened risk of mortality will be stronger in males than females. Males are typically more susceptible to predation due to a complex set of factors (including being larger, more colorful, and display more frequently; Zuk and Kolluru 1998). This trend has also been shown in lizards (Husak et al. 2006; Costantini et al. 2007). In *U. stansburiana* the heightened susceptibility to predation may be more pronounced because males are larger and more conspicuously colored, characteristics that lead to sexually disparate predation pressure in other species (Stuart-Fox et al. 2003; Husak et al. 2006). Males also tend to be more active and active during more hours of the day (Irwin 1965; Tinkle 1967), which likely increases predation risk.

Prediction 2: Home range or territory size

Across many lizard taxa, males aggressively defend territories in order to gain and protect their access to females. Males typically occupy larger spaces than females (Stamps 1977; Rose 1982; Perry and Garland 2002; Stone and Baird 2002). Most studies with lizards found a correlation between male size and territory size (reviewed in Pianka and Vitt 2002; but see Bull and Freake 1999; Van Sluys 1997 for exceptions). Tail autotomy immediately reduces total body size of the lizard, and therefore, may affect ability of the tailless lizards to retain a territory of maximum size. In other studies, tail autotomy led to decreased territory size in a semi-natural setting for the lizards *Psammadromodus algerius* (Salvador et al. 1995) and *Lacerta monticola* (Mártin and Salvador 1997), but no effect was detected in *Anolis sagrei* (Kaiser and Mushinsky 1994). Fox and McCoy (2000) suggested that males in the western Texas population of *U. stansburiana* may abandon territoriality and assume a sneaker strategy following loss of the tail. If tailless males are indeed acting as sneakers, they should abandon territorial defense and expand their home range to encounter more females. We predict that tailless *U. stansburiana* males will inhabit larger home ranges than their tailed counterparts and that tail autotomy in females will have no effect on home range size. Furthermore, we predict that this shift can occur during a single breeding season, can happen after individuals have already established territories, and will not be related to other measures of body condition.

Prediction 3: Home range overlaps

Lizard territories and home ranges typically contain areas of both inter- and intrasexual overlap, with considerable variation in the number and extent of overlaps among individuals. The territories of polygynous males typically overlap more female home ranges, which provides greater opportunities for reproductive success. Typically, male *U. stansburiana* in western Texas actively defend territories that exhibit little overlap with other male territories and extensive overlap with the home range of one female (Tinkle 1967). We predicted that the territories (home ranges) of tailless sneaker males will overlap the home ranges of more neighboring females, allowing them to maintain fitness levels similar to their tailed (strictly territorial) counterparts. Tail autotomy causes shifts in behavior in *U. stansburiana* consistent with a sneaker strategy. Thus, following tail autotomy the number of home ranges overlapped by tailless males will be greater than the number of home ranges overlapped by tailed males. *Uta stansburiana* females are also territorial (Tinkle 1967), but the tail is used primarily to signal social status (Fox et al. 1982; Fox et al. 1990). Females, therefore, fight less for territory than do males. Tailless females are predicted to maintain the same number of home range overlaps after tail autotomy because females, tailed or tailless, are virtually guaranteed to acquire a mate and therefore, the tail should have little impact on the maintenance of female home ranges.

Prediction 4: Home range microhabitat diversity

A lizard's home range must provide basic resources (i.e., access to mates, food, and basking and nesting sites, and protection from predators and stressful environmental conditions). Lizards attempt to maintain home ranges that optimize access to these resources. For this population of *U. stansburiana*, environmental conditions are extreme: long, hot, dry and windy summers, with shorter, but intensely cold, winters, sparse vegetative cover, and an abundance of different predators with different hunting modes. Home range quality can be gauged by examining microhabitat diversity. *Uta stansburiana* is a generalist both in habitat choice and prey selection (Tinkle 1967; Parker and Pianka 1975; Conant and Collins 1998; Jones and Lovich 2009). Thus, it is assumed that having a more diverse vegetative community plus other structures in the home range of an individual is beneficial. In fact, home range microhabitat diversity has been shown to accurately predict juvenile *U. stansburiana* survivorship in this population (Fox 1978; Fox 1983).

Therefore, we used microhabitat diversity within each individual's home range can serve as an indicator of home range quality. We predicted that tail autotomy would negatively affect on the ability to defend an area with greater diversity, and therefore, tailless individuals would be socially relegated to use less diverse habitats. Again, we predicted that this effect would vary by sex. Tailless males were predicted to lose access to the most important, or rarest, resources. Tailless females were predicted to signal their subordinate status (due to lack of a tail) and be relegated to suboptimal areas, but to a lesser degree than tailless males. It should be noted that males and females likely view different plant communities, structures, and levels of diversity as optimal.

Prediction 5: Distance moved between sightings and number of days between sightings

Tail autotomy has been shown to lower the amount of time spent in the open, decrease locomotor performance, compromise foraging ability, and decrease activity levels (reviewed in Bateman and Fleming 2009). *Uta stansburiana* is strongly molded by sexual selection and exhibits sexually disparate effects of tail autotomy on sprint performance (Anderson et al. 2012) and foraging behavior (Anderson Previous Chapter). We predicted that the number of movements and the frequency of sightings (inversely, days between sightings) would also affected by tail loss. Male *Lacerta monticola* moved less frequently and over shorter distances after tail loss (Mártin and Salvador 1993a). These tailless males continued to attempt to defend territories; they modified their spacing and movement behavior without assuming a sneaker strategy. In our study, tailless males, if they assume a sneaker strategy, should move longer distances but be sighted less frequently. Tailless males behave less conspicuously, and thereby, avoid detection by, and conflict with territorial males (Anderson Previous Chapter). Tail loss in females has been shown to lead to more foraging attempts (Anderson Previous Chapter), but this may not affect the distance moved within the home range as attempted prey captures occur over very short distances (< 1 m). The behavior of *U. stansburiana* also leads to the prediction that male and females will move around their home ranges, and be sighted foraging and basking, at different rates (as reported by Tinkle 1967). We predict that tail loss will increase this difference between the sexes.

MATERIALS AND METHODS

Study animal.— *Uta stansburiana* is a small, widely distributed lizard species of the southwestern United States and northern Mexico (Conant and Collins 1998; Stebbins 2003; Jones and Lovich 2009). Not only is *U. stansburiana* widely distributed, but it is also one of the most common lizards of the desert southwest. Population densities can be quite high in areas of appropriate habitat (Tinkle 1967; Parker and Pianka 1975; Scoular et al 2011). These lizards are small (maximum SVL = 57 mm and mass = 6.5 g; Tinkle 1967). Due to its small size, relative abundance, and active life-style, *U. stansburiana* experiences intense predation from a variety of predators with different hunting modes. Strong sexual dimorphism is also evident in *U. stansburiana*; males are larger in measures of snout-to-vent length (SVL), tail length, head width, and head length, and are heavier (Table 1). The sexes also show sexual dichromatism, with males being more colorful, often having turquoise flecks over the body and down the dorsum of the tail, and exhibiting a varying array of throat colors. In males, these throat colors have been linked to an evolutionarily stable strategy (ESS) of three social strategies (rock-paper-scissors game) in at least one population, potentially many more (Sinervo and Lively 1996; Corl et al. 2010). *Uta stansburiana* is insectivorous, and employs a sit-and-wait ambush strategy. However, lizards frequently shift from one ambush site to another throughout the day. The sexual differences in *U. stansburiana* extend to differences in diet (Best and Gennaro 1984), with males eating a larger range, both size and variety, of prey items. Presumably, this is tied to overall larger size of males, especially in the head.

Territories are maintained by both males and females (Tinkle 1967; Fox 1978; Fox 1983). Territorial defense consists of a stereotypical set of behaviors, mainly pushup and headbob displays, but can lead to fights, resulting in biting and chasing. Even so, the most intense fights between male *U. stansburiana* are relatively mild and rarely result in injury. Polygynous males attempt to maintain a territory which overlaps as many female territories as possible, while excluding other males (Tinkle 1967; Fox et al. 1981; Fox 1983). Females also defend quality habitat, but use the tail as a status badge and do not fight as frequently or intensely (Fox and Rostker 1982; Fox et al. 1990). Females lay multiple clutches of 3-4 eggs during the short breeding season (Tinkle 1967).

At our study site, *U. stansburiana* is virtually an annual species, with less than 10% of the adults surviving to a second breeding season (Tinkle 1967; Anderson Pers. Obs.). Both males and females must maximize fitness and mating opportunities during their single breeding season. Presumably, males (i.e., tailed ones) increase fitness by sequestering and courting females within their territory, and females increase fitness by increasing the number of clutches and subsequently depositing these clutches in optimal nesting sites.

Study site.— The study site was located in western Texas in Winkler Co., 7 km southeast of the town of Kermit (31.75916 N 102.970083 W) on a large cattle ranch, which also supports a large oil and natural gas extraction operation field. This area is within a belt of active, sparsely vegetated, sand dunes that extend from southeastern New Mexico into western Texas (Fig. 1). The dunes are windblown and are constantly shifting. They are mostly open sand, with pockets of vegetation. Dune edges are stabilized by vegetation, especially the diminutive Havard Shin Oak (*Quercus havardii*). The shin oaks' extensive root system effectively anchors the sand grains, thereby forming the dome-shaped coppice dunes. *Uta stansburiana* prefers the vegetated edges of stabilized dunes, and is infrequently sighted in more open, active dunes. Overall, vegetative cover is sparse, with some estimates of over 60% bare ground even in these edge areas (Machenberg 1984).

The vegetative community along the edges of the dunes consists of disjunct patches of bunch grasses (several species, including *Sporobolus*) and small forests of shin oak, with clumps of mesquite (*Prosopis glandulosa*), yucca (*Yucca glauca*), and broomweed (*Amphiachyris dracunculoides*) occurring less frequently. *Uta stansburiana* uses all of these plant types at various times for refuge, either from predators or weather. The dunes occur in an ecotone between the extreme southern tip of the Great Plains and the northernmost reaches of the Chihuahuan Desert (Machenberg 1984). The effects of cattle grazing and ranch activity play a major role in the types and distributions of plants found in this region; care was taken that the study site was representative of the overall plant community in western Texas.

Uta stansburiana can be found aboveground in every month of the year at the site, depending on air temperature (Tinkle 1967). However, the active season stretches from late February until late October in most years (Tinkle 1967; Anderson Pers. Obs.). During the early half of this active season, only adult lizards are present. Beginning in early August, until the end of the active season, almost all lizards seen are juveniles (Anderson Pers. Obs.). Very little joint presence of adults and juveniles occurs. When lizards emerge in the early spring, almost all are sexually mature and immediately establish territories and begin searching for mates. The breeding season lasts from early March until June.

The climatic conditions at this site during the breeding season are extreme and can be characterized as hot, dry, and windy. Mean daily temperatures range from 4- 37^{0}C, with daily highs often > 40°C. As is common in semiarid regions, rainfall is unpredictable, but never frequent. Most of the precipitation falls in the spring and early summer during localized thunderstorms. The dunes experience frequent and sometimes intense winds (> 50 km/h sustained). These winds fuel the movement and deposition of the sands that form the dunes (Machenberg 1984).

Blowouts are areas where the force of the winds has created a barren depression within an otherwise vegetated patch of dunes. These blowouts can act as basins for the infrequent rainfall and when filled with rainwater are called swells. However, *U. stansburiana* seems to avoid blowouts and swells. This unique combination of geological, vegetative, and climatic factors influences the behavioral ecology, especially territorial behavior, of this population of the side-blotched lizard.

The study plot consisted of approximately 4 ha of habitat along the western edge of an active set of dunes (Fig. 2). This plot was surveyed daily from mid-March to early June during 2008 and 2009. The surveys consisted of random walks through the plot. Our presence and movements would often force lizards to abandon an ambush site and flee to the nearest refuge. The lizard was then captured, or if already marked, individual identification was determined.

Lizards were captured using a portable mesh trap with a v-shaped opening (Fox 1978). The number of lizards and their sex ratio were consistent between years (2008: 87 males, 101 females; 2009: 62 males, 96 females). For individual identification, each lizard was assigned a unique toe clip, and a color coded four-dot combination was painted on the dorsum using non-toxic acrylic paint (Fox 1978). At initial capture, morphological measurements were made (Table 1). Lengths were measured with a flexible ruler (± 1 mm) and mass measured with a spring-loaded Pesola scale (± 0.25 g). Sex was determined based on the presence or absence of secondary sexual characteristics (body coloration or the presence of enlarged post-cloacal scales in males). The series of dorsal painted dots were easily discernible in the field with the aid of binoculars and allowed for individual recognition without the need for recapture. Paint had to be reapplied infrequently during the season. During the daily surveys, all unmarked lizards were captured and processed in the field as described above.

Each sighting of a marked lizard was georeferenced using a hand-held GPS unit, in 2008 a Garmin (eTrex HC) and in 2009 both the Garmin and a Trimble (Geo XH). These georeferenced sightings were used to estimate home range size using the minimum convex polygon (MCP) method. Also at each sighting the lizard's initial location was categorized into one of nine available microhabitats: open sand, shin oak, grass, yucca, broomweed, mesquite, rock/gravel, other plant, or debris (Table 2). These categories represent the major types of vegetation and structure available at the site. These same categories were used in the microhabitat diversity assessment.

At the beginning of each year when we first captured lizards so that we could establish our treatment and control groups, we made measurements of all lizards (Table 1). In this total set of lizards, some animals either had a completely intact, unbroken tail or they had lost a portion of their tail due to predator-induced tail autotomy. These natural tail loss events occurred as a result of predation and the time since break and amount of regeneration length varied greatly. The length of the regenerated tail was measured from cloaca to break point and denoted as the natural tail break length; NatTBL (Table 1). Neither the number, nor proportion, of natural tail breaks differed between males and females (males: n = 53; females: n = 56; $\chi^2 = 0.83$, df = 1, p = 0.774), nor was NatTBL correlated with SVL in either sex (males: Pearson r = 0.123, n = 148, p = 0.148; females: Pearson r = 0.085, n = 192, p = 0.192).

Our field experiment occurred in two distinct and sequential phases (Fig. 3). In the first, or Pre-phase (6 weeks of daily surveys), all lizards with > 6 sightings and fully intact tails became subjects. Six sightings is consistent with, or slightly higher than the minimum number, used in other studies that estimated home range size for *U. stansburiana* using the minimum convex polygon (MCP) method (Tinkle 1967; Rose 1982; Scoular et al. 2011). The pros and cons of the MCP method compared to other procedures to estimate home range size are detailed elsewhere (Rose 1982; Worton 1987; Lawson and Rodgers 1997; Perry and Garland 2002; Stone and Baird 2002; Laver and Kelly 2008), and we will not attempt to expound on this subject further. To confirm that six sightings would provide a good estimate of home range size, we plotted the ln home range area against the number of sightings (Fig. 4). Home range size using six sightings seems to be near the asymptote of the relationship between ln home range area and number of sightings. Thus, we feel confident using a minimum of six sightings to estimate home range area using the MCP technique. Most subjects were seen more times than this minimum (mean ± 1 SD =9.32 ± 3.01 sightings). After 6 weeks, we had accumulated a total of 396 and 489 sightings of our subjects in 2008 and 2009, respectively. We were then able to use these sightings to estimate home range size, overlap, distance traveled between sightings, and the mean number of days between sightings for the Pre-phase for all subjects.

At the mid-point in the breeding season (mid-April; Fig. 3), all of the subject lizards were captured and half of the lizards were released immediately; this group acted as a control. The other half, the treatment group, was forced to autotomize a portion of the tail. The experimenter applied gentle pressure to the tail using the thumb and forefinger. This pressure was enough to induce autotomy. Autotomy is an active process, and lizards could not be anesthetized during the procedure. Effort was made to insure that the autotomy removed approximately the distal two-thirds of the tail--each treatment lizard had the tail break length measured, ExptTBL (Table 4).

Estimates of home range area were computed using the 95% MCP calculated from these Pre-phase sightings. The software package *Ranges* ver. 8.0 (Anatrack Ltd.) was used to calculate area (m^2) and to count the number of overlaps (n) with neighbors. From these geo-referenced sightings, the average distance (m) moved between sightings was also obtained for each subject. The number of days between consecutive sightings in each phase was determined for each lizard. From these, we calculated the mean days between observations (MDBO). The total number of survey days for the experiment was similar between years (2008 n = 70; 2009 n = 69).

The MCP was then physically demarcated in the field using the GPS unit, contractor flags and string. At this time, a visual estimate of the percent coverage of each of the microhabitat types within the demarcated area was completed based on the methods presented by Fox (1978). These percent estimates of cover were used to calculate an index of microhabitat diversity within the home range, using the Shannon-Weiner (H’) index (sensu Fox 1978).

After these estimates and tail autotomies were completed, daily surveys were continued using the same methods described for the Pre-phase. All individuals were identified and georeferenced during this, the Post-phase. After an additional 6 weeks, all surviving subjects with 6 or greater sightings in the Post-phase again had their home ranges demarcated and an estimate of home range diversity was made. The same procedures for estimating home range size and the number of overlaps, diversity, average distance moved between sightings, and MDBO were followed, based exclusively on Post-phase sightings (Fig. 3).

To assess the maximum extent of a lizard's home range, an additional measure of home range size was also calculated in *Ranges*. All sightings (Pre- and Post-phase) were combined and a measure of home range size from this full set of sightings was calculated and defined as total home range. Measures of total home range may reveal either territorial compression due to pressure from neighbors or territorial expansion as part of an alternate strategy (i.e., sneaker).

From sightings, we were able to calculate the average distance moved between sightings by individuals. This distance can act as a surrogate for territorial behavior. By assessing the distances moved during the Pre- and Post-phases, a comparison of movements between tailed and tailless individuals can be made.

Statistical design.— The study design allowed us to contrast the changes in home range quality (size, number of overlaps, and microhabitat diversity) and movement characteristics from Pre- to Post-phase in tailed and tailless individuals, using a two-step approach. First, the tail status groups (tailed [control] and tailless [treatment]) were compared with each other separately for the two phases of the experiment using independent samples *t*-tests. During the Pre-phase (when all lizards have intact tails), the control and treatment groups were predicted to be similar in all measures of home range quality. Then the same comparisons between groups in the Post-phase were made, to determine if the treatment lizards developed different home range and movement characteristics as a consequence of tail loss.

The second step assessed within-group effects over the course of the experiment using Wilcoxon Matched-Pairs Signed-Ranks Tests. This test detects changes from Pre- to Post-phase within a group (e.g., if treatment males decreased microhabitat diversity over time). The null hypothesis is that the direction (positive or negative), or significance, of any change in the control group (a natural temporal change) should be mirrored by the treatment group. If the direction, or significance, is not matched by the treatment group, then tail loss has affected the ability to acquire or maintain that territorial or home range characteristic. All statistical comparisons were made using SPSS, version 18.0 (IBM Corp.).

RESULTS

The number of resident lizards with > 6 sightings in the Pre-phase was consistent between the years (2008: 16 males, 21 females; 2009: 19 males, 26 females). The number of subjects surviving to the end of the breeding season (2008: 12 males, 11 females; 2009: 17 males, 14 females) was also consistent between years. The sizes of subject lizards did not differ between 2008 and 2009 for any morphological variable (Table 3). Consequently, the years were pooled for all subsequent analyses. As expected, we found clear sexual dimorphism in size. Males were significantly larger than females in every size measure (all $p < 0.05$). However, control and treatment lizards within each sex did not differ in size (t-tests: all $p > 0.05$; Table 4). The sex ratio was skewed, with more females in the initial subject group ($\chi^2 = 5.760$, df = 1, p = 0.016); however, the sexes were always analyzed separately. The two groups (control and treatment) did not differ in their number of sightings in the Pre-phase of the study (see Table 3).

Prediction 1: Survivorship

Control male *U. stansburiana* that retained their tail, the control group, were more likely to survive through the breeding season than their tailless counterparts (treatment group), and this was statistically significant if the α level was set at 0.10 for this Chi-squared test because of the directionality of the prediction (Chi-squared tests are always 1-tailed but measure goodness of fit for deviations in either direction from expected) ($\chi^2 = 3.457$, df = 1, p = 0.063). In females the pattern was more pronounced, more tailed females survived the breeding season than tailless females (again the α level for significance was set at 0.10 because of the directionality of the prediction ($\chi^2 = 4.787$, df = 1, p = 0.029). For all subsequent analyses, only lizards which survived to the end of the Post-phase were included; these survivors had both Pre- and Post-phase scores for all measurements taken.

Prediction 2: Home range size

Home range size (m^2) was not normally distributed, with a right-skewed distribution for both males and females. To correct this deviation from normality, all home ranges were natural log (ln) transformed. Males had significantly larger home ranges than females during the Pre-phase of the study (2-tailed t-test: $t_{52} = 2.474$, $p = 0.017$), approximately double that of females (Table 5). Home range size in males was not correlated with SVL (Pearson correlation r = 0.160, n = 41, p= 0.316).

Control and treatment males had similar-sized home ranges during the Pre-phase (2-tailed t-test: $t_{21} = 1.030$, p = 0.315). Over the course of the breeding season, tailless males increased the size of their home range by ca. 100 m^2 while their tailed counterparts contracted theirs by ca. 225 m^2 (Table 5). Post-phase home range sizes of these groups were statistically significant in the predicted direction (1-tailed t-test: $t_{21} = 1.989$, p = 0.03). Mean home range size increased for the treatment group males from the Pre-phase (475 m^2) when they had intact tails to the Post-phase (570 m^2) following experimental tail removal. Removal of a substantial portion of the tail, however, did not elicit a statistically significant increase in home range size (m^2) in tailless male

U. stansburiana (1-tailed Wilcoxon test: Z = -0.175, *P* = 0.431). For tailed males the mean size of home range decreased from the Pre-phase (425 m^2) to the Post-phase (200 m^2), and appears biologically different. However, this change was not statistically significant, either (2-tailed Wilcoxon test: Z= -1.070, P = 0.285). Although the differential changes in home range size from the Pre- to Post-phase for tailed and tailless males analyzed separately were not statistically significant, a clear biological trend is evident and the direct comparison of tailed vs. tailed males in the Post-phase was statistically significant. Tailless males were expanding their home ranges at the same time as tailed ones were contracting theirs.

During the Pre-phase, control and treatment female *U. stansburiana* had similarly sized home ranges (2-tailed t-test: t_{29} = -0.391, p = 0.698). As in males, home range size in females was not correlated with female body size (Pearson correlation r = 0.125; n = 54, p = 0.366). Both tailed and tailless females decreased their home range size over the course of the breeding season by ca. 75 m^2 (Table 5). The Post-phase home range size of the two groups remained statistically similar (2-tailed t-test: t_{29} = 0.919, p = 0.366). Mean home range sizes were similar for the treatment group females during the Pre-phase (230 m^2) when they had intact tails and the Post-phase (160 m^2) following experimental tail removal (2-tailed Wilcoxon test: Z= -1.067, *P* = 0.286; Table 5). For tailed females, the mean home range sizes in the Pre-phase (240 m^2) and the Post-phase (160 m^2) appear biologically similar and were not significantly different (2-tailed Wilcoxon test: Z= -1.852, P = 0.064; Table 5). The total home range area (the maximum area occupied by a lizard during the entire breeding season) was significantly different between control and treatment males Tailless males had larger total home ranges than their tailed counterparts (1 tailed t-test: t_{19} = 2.198, *p* = 0.02), with an average total home range approximately two times as large as the tailed ones (Table 5). This was not true for female total home range size (2-tailed t-test: $t_{28} = 0.016$, $p = 0.981$).

Prediction 3: Home range overlaps

Home ranges can overlap neighbors of either the same, or the opposite sex. The reason and potential consequences of these types of overlap are clearly different. Therefore, the strategies employed by the sexes should differ; i.e., males would benefit from overlap with many females, while minimizing overlap with males. Females would benefit from less overlap of both sexes (as long as they were overlapped by at least one male). We compared the same and opposite sex overlaps for all resident lizards, both during the Pre- and Post-phases of the study.

For males, the number of overlapping home ranges during the Pre-phase did not vary between the years of the study. Both male-male overlaps (2-tailed t-test: $t_{21}= -0.123$, $p = 0.899$) and male-female overlaps (2-tailed t-test: $t_{21} = -0.973$, $p = 0.341$) were similar in 2008 and 2009. This was also the case during the Post-phase, the number of male-male (2-tailed t-test: $t_{21} = -0.256$, $p = 0.800$) and male-female (2-tailed t-test: $t_{21} = -0.945$, $p = 0.355$) home range overlaps were similar for males during both years. Therefore, years were pooled in subsequent analyses.

Treatment and control male lizards did not differ in the number of male-male (2-tailed t-test: $t_{21} = 0.126$, $p = 0.901$) nor male-female (2-tailed t-test: $t_{21} = 0.303$, $p = 0.765$) overlaps during the Pre-phase, when all individuals had fully intact tails. At the end of the breeding season, the two groups (treatment and control), continued to have the same number of male-male (1-tailed t-test: $t_{21} = 1.091$, $p = 0.145$), and male-female (1-tailed t-test: $t_{21} = 1.385$, $p = 0.091$) overlaps. Males that retained their tail throughout the study significantly decreased the number of male-male (2-tailed Wilcoxon test: $Z = -2.124$, $p = 0.034$) and the number of male-female (2-tailed Wilcoxon test: $Z = -2.254$, $p = 0.024$) overlaps (Table 6). On the other hand, tailless males did not increase their overlap as predicted, neither for number of male-male overlaps (2-tailed Wilcoxon test: Z = -1.259, p = 0.208) nor male-female overlaps (2-tailed Wilcoxon test: Z = -1.743, p = 0.081). In fact, both same and opposite sex overlaps decreased (Table 6), but not significantly so and not as much as the tailed males.For females, the number of overlapping home ranges during the Pre-phase did not vary between the years of the study. Both female-female overlaps (2-tailed t-test: t_{34}= -0.968, p = 0.340) and female-male overlaps (2-tailed t-test: t_{34} = 0.247, p = 0.806) were similar in 2008 and 2009. This was also the case during the Post-phase. Female-female (2-tailed t-test: t_{34} = 0.001, p = 0.999) and female-male (2-tailed t-test: t_{34} = -1.300, p = 0.202) overlaps were similar during both years. Therefore, years were pooled in subsequent analyses.

Treatment and control female lizards did not differ in the number of female-female (2-tailed t-test: t_{34} = 0.920, p = 0.365) nor female-male (2-tailed t-test: t_{34} = 0.441, p = 0.663) home range overlaps during the Pre-phase, when all individuals had fully intact tails. At the end of the breeding season, the two groups of females (treatment and control), continued to have the same number of female-male (2-tailed t-test: t_{29} = 0.759, p = 0.454), and female-female (2-tailed t-test: t_{29} = 0.228, p = 0.821) overlaps.

Females that retained their tail through the Post-phase, as well as tailless ones, decreased the number of female-female (tailed: Wilcoxon Z = -1.732, p = 0.083; tailless: Wilcoxon Z = -1.664, p = 0.096) and female-male (tailed: Wilcoxon Z = -1.642, p = 0.101; tailless: Wilcoxon Z = -1.231, p = 0.218) overlaps, but none of these decreases in overlap were statistically significant.

Prediction 4: Home range microhabitat diversity

There was no statistically significant difference between the H' diversity scores for the Pre-phase between 2008 and 2009 for males (2-tailed t-test: $t_{23} = -0.410$, $p = 0.686$) or females (2-tailed t-test: $t_{34} = -0.379$, $p = 0.707$). Therefore, we pooled the years for subsequent analyses. The H' for the Pre-phase was not correlated with the Pre-phase home range size for males (Pearson Correlation $r = 0.618$, $n = 25$, $p = 0.423$) or females (Pearson Correlation $r = -0.020$, $n = 36$, $p = 0.907$).

At the end of the Post-phase, a second diversity survey was completed for all surviving subjects. A statistically significant difference between the H' scores for the post phase between 2008 and 2009 was not detected for males (2-tailed t-test: $t_{23} = -1.331$, $p = 0.196$) nor females (2-tailed t-test: $t_{34} = 0.856$, $p = 0.398$); therefore, we pooled the years for subsequent analyses. The H' for the post-phase was not correlated with the post-phase home range size for males (Pearson Correlation $r = 0.294$, $n = 25$, $p = 0.153$) nor females (Pearson Correlation $r = -0.049$, $n = 36$, $p = 0.777$).

Control and treatment lizards had similar diversity within their home ranges during the Pre-phase when all individuals had fully intact tails (2-tailed t-test for males: $t_{21} = 0.351$, $p = 0.729$; 2-tailed t-test for females: $t_{28} = 0.544$, $p = 0.591$). Through the season, tailed males' home range diversity significantly increased (2-tailed Wilcoxon test: $Z = -1.988$, $p = 0.047$), whereas that of tailless males decreased, but not significantly so as predicted (1-tailed Wilcoxon test: $Z = -1.363$, $p = 0.087$). Comparing the groups directly, tailless males had significantly less diversity within their home ranges in the Post-phase than their tailed counterparts (1-tailed t-test: $t_{21} = 0.985$, $p = 0.017$). In females on the other hand, the microhabitat diversity within the home ranges of both the control and treatment groups decreased through the breeding season (Table 7), but this decrease was statistically significant (2-tailed tests) only in control females (tailed:

Wilcoxon Z = -2.040, p = 0.041; tailless: Wilcoxon Z = -1.023, p = 0.306). When compared directly, these decreases in diversity did not lead to statistically significant differences in Post-phase diversity between control and treatment females (2-tailed t-test: $t_{27} = 0.692$, p = 0.495).

Prediction 5: Distance moved between sightings and number of days between sightings

Distance moved was calculated by measuring the average distance moved between consecutive sightings for each lizard. This is a straight-line distance and obviously must be considered the minimum distance moved, but we assume there is no bias in one group or another when analyses are made. The control and treatment males moved similar distances during the Pre-phase (2-tailed t-test: $t_{21} = 0.221$, p = 0.827) when all individuals had fully intact tails. The mean distance moved between sightings during the Pre-phase was 16.4 m for the treatment and 15.4 m for the control group (Table 8). In the Post-phase, tailless males moved significantly greater distances between sightings than tailed males, as predicted (1-tailed t-test: $t_{21} = 1.851$, p = 0.039). Tailless males moved on average 19.4 m, and tailed males moved 10.6 m (Table 8).

The two groups of females moved similar distances between sightings during the Pre-phase (2-tailed t-test: $t_{29} = -0.364$, p = 0.719) when all individuals had fully intact tails. The mean distance moved during the Pre-phase was 12.0 m for the control and 11.4 m for the treatment group (Table 8). In the Post-phase, tailed and tailless females again moved similar distances (2-tailed t-test: $t_{29} = -0.393$, p = 0.697). Tailless females moved on average 10.3 m between sightings, whereas the tailed females moved 11.1 m during the Post-phase.

The number of days between consecutive sightings for each individual was calculated, and the mean days between observations (MDBO) determined for each subject in the Pre- and Post-phase. A decrease in MDBO means the individual is being sighted more frequently. The control and treatment males had similar MDBO during the Pre-phase (2-tailed t-test: $t_{22} = 0.66$, p

= 0.511) when all individuals had fully intact tails. The MDBO during the Pre-phase was 3.30 days for the control and 2.96 days for the treatment groups of males (Table 8). In the Post-phase, tailless males did not have significantly greater MDBO than tailed males, as predicted (1-tailed t-test: $t_{22} = -0.063$, $p = 0.475$). Males in both groups showed a gradual, but not statistically significant, decrease in MDBO (thus, 2-tailed tests for each) from the Pre- to the Post-phase (Wilcoxon test: control $Z = -1.886$, $p = 0.059$; treatment $Z = -1.915$, $p = 0.056$; Table 8). In the Post-phase, males had decreased MDBO to a point that control males were sighted on average every 2.25 days and treatment males every 2.27 days.

The control and treatment females had similar MDBO during the Pre-phase (2-tailed t-test: $t_{29} = 0.494$, $p = 0.625$) when all individuals had fully intact tails. The MDBO during the Pre-phase was 3.43 days for the treatment and 3.77 days for the control groups of females (Table 8). In the Post-phase, tailless females had similar MDBO as the tailed females, as was predicted (2-tailed t-test: $t_{29} = -0.145$, $p = 0.826$). Females, both tailed and tailless, decreased their MDBO over the course of the experiment, but this change was statistically significant only in tailless females (2-tailed Wilcoxon tests: control $Z = -1.664$, $p = 0.096$; treatment $Z = -2.675$, $p = 0.007$). In the Post-phase, control females were observed on average every 2.47 days and treatment females every 2.41 days.

DISCUSSION

There are numerous lines of evidence suggesting that tail autotomy in lizards negatively affects the physiological and behavioral characteristics necessary to obtain and defend optimal territories. Tailless individuals are typically slower (Ballinger et al. 1979; Punzo 1982; Formanowicz et al. 1990; Mártin and Avery 1998; Downes and Shine 2001; Chapple and Swain

2002; Copper Jr. et al. 2004; Anderson et al. 2012) and have lower endurance than tailed counterparts (Daniels 1985; Mártin and Avery 1998; Chapple and Swain 2002). A decrease in speed or endurance might hamper a territorial individual from successfully defending its territory. Slow lizards cannot intercept and escort intruders out of their territory as quickly and individuals with less stamina may not respond to every intrusion. Tailless individuals are less active (Salvador et al. 1995; Cooper Jr. 2003; Formanowicz et al. 1990; Downes and Shine 2001); therefore, they might spend less time defending their territory, and are more susceptible to invasion by neighbors. The tail typically contains stores of fat reserves and the process of regenerating the tail is energetically costly, causing tailless individuals to forage more often (Dial and Fitzpatrick 1981; Anderson Previous Chapter) and have less energy to use for courtship and social interactions (Dial and Fitzpatrick 1981; Wilson and Booth 1998). Tailless *U. stansburiana* are less aggressive in dyadic encounters (Fox et al. 1990) and this lowered aggressiveness may reduce competitive ability both in intrasexual and intersexual interactions related to space use (Mártin and Salvador 1993a; 1993b). The additional costs of tail autotomy are numerous, and synergistically they reduce survivorship and reproductive fitness (reviewed in Bateman and Fleming 2009).

Few studies have addressed the cost that tail autotomy has on the ability to acquire, or defend, an optimal territory. It has been suggested in *U. stansburiana* that tailless males assume a sneaker strategy following tail loss (Fox and McCoy 2000). If males give up territory defense and attempt to gain copulations from sneaking onto neighboring males' territories, then the sneaker male might be able to maintain levels of fitness equal to its neighbors, or at the very least minimize the fitness costs associated with tail loss. Female *U. stansburiana* can signal lowered status using the absence of the tail (Fox and Rostker 1982; Fox et al. 1990), and fight less

(Anderson Previous Chapter), effectively accepting lower, or suboptimal, quality home ranges. This option is not available to the males.

The costs listed above, and the suggestions of Fox et al. (1990) and Fox and McCoy (2000), led to the testable predictions presented in this study. We examined the changes in territory size, overlap, and quality, and movement behavior of residents following tail autotomy by measuring these characteristics before and after induced tail autotomy. We predicted that the sexes would show clearly different responses following tail autotomy. *Uta stansburiana* is strongly molded by sexual selection, leading to sexually disparate morphology, coloration, and behavior. It is reasonable to think that the response to tail autotomy also would be different between the sexes. A recent example of this sexually disparate response to tail autotomy was seen in sprint performance. Tail autotomy significantly decreased sprint performance in female *U. stansburiana*, but not males (Anderson et al. 2012). It was suggested that males somehow compensate for tail loss and maintain sprint speed because of their need for maximal sprinting ability for territorial defense.

We predicted that tail autotomy would lower survivorship during the relatively short breeding season, more so in males than females. Following the experimental autotomization of a portion of the tail, male survivorship significantly declined, as did female survivorship, and even more sharply. The fact that female survivorship fell more than male survivorship runs counter to our prediction. Tailless individuals have lost the valuable antipredatory tactic of autotomy for future avoidance of predation. However, the increased mortality experienced by females did not occur only due to predation, presumably some died from starvation, desiccation, disease, or stress (but all of these should affect males and females equally). Tailless females may have been affected more by other pressures associated with the breeding season, e.g., egg production, nest excavation, and egg-laying. Tailless females continue to lay the same number and size of eggs as their tailed counterparts (Fox and McCoy 2000), but they are energetically and behaviorally compromised by the lack of a tail. Tailless females have been shown to forage more frequently, but without producing more fecal output (Anderson Previous Chapter). The energetic burdens of tail regeneration, combined with egg production, may combine to increase mortality in tailless females. Males avoid this increase in mortality due to the relatively cheap physiological costs of sperm production. We predicted that tailless males would experience more predation pressure, and subsequently increased mortality, because as sneakers they need to move around more often, and would be traversing unfamiliar areas to find unattended females. Tail autotomy affects refuge use and flight initiation distance, so traveling in unfamiliar areas would only exacerbate this cost (Cooper Jr. 2003; Cooper Jr. 2007). Fox and McCoy (2000), measuring survivorship of tailed and tailless *U. stansburiana* over a longer period, found significantly lower survivorship in tailless males compared to tailed ones, but not so in females. Following tail loss, if males assume a sneaker strategy, they should abandon territoriality and increase the size of their home range. As such, sneakers would increase the likelihood of encountering more females. Those females would typically be defended by and located within the territories of other males, likely tailed ones. Tailless females, on the other hand, should follow a similar pattern of behavior as tailed females. The tail is known to act as a status badge in female *U. stansburiana* (Fox and Rostker 1982; Fox et al. 1990). Therefore, tailless females can be relegated to lower status without having to abandon their territory (or shift to nearby inferior areas, but not necessarily expand the size of their territory). Our predictions for males and females both held true. Tailless males increased the size of their home ranges and ultimately occupied a significantly larger area than their tailed counterparts. The magnitude of this size difference was impressive. During the breeding season, tailed males decreased home range area by almost 100 m^2, whereas tailless males actually increased their home range area by 225 m^2, a net change of over 325 m^2 between tailed and tailless males. In this study, tailed and tailless females decreased the size of their home range over time. This decrease in territory size by tailed males and all females represents a contraction and consolidation of territory, probably because of decreased need for large territories as the breeding season draws to a close. After losing a portion of the tail, the treatment males were forced out of their core territorial areas by more assertive and aggressive tailed neighbors. This lead to abandonment of territoriality and expansion of the home range of the tailless males to ensure overlaps with more females (thereby increasing potential sneak copulations) in order to maintain fitness.

Following tail loss, males (acting as sneakers) should increase the number of overlaps with opposite sex neighbors. As they do this, sneaker males will be forced to overlap also with numerous other male territories. The sneakers can avoid increased conflict by abandoning territoriality. Territorial males tend to do the opposite; they overlap very few females, and competitively exclude other males. Initially, all males overlapped several neighboring home ranges, on average two male and three female neighbors. But over the breeding season, tailed males decreased their number of overlaps to an average of only one male and one female neighbor. The tailless males, however, did not decrease overlaps over time. They maintained multiple overlaps (on average 1-2 males and 2 or more females) throughout the season. This pattern matches the trend of increased home range size in tailless males, while the tailed males were contracting their territories. Over the course of the breeding season, tailed males focused their energy on defending a smaller territory with fewer male or female overlaps. Tailed males can maximize their exclusivity to a smaller number of females by making their territories smaller. This also lowers the number of neighboring males the tailed males overlap. Tailless males did the opposite. They appeared to abandon territoriality and increased their home range size, thus continuing to overlap with multiple neighbors, both male and female. It seems that tailless males trade the costs of maintaining overlaps with male neighbors for the potential benefit of overlap with more female neighbors. This indicates that tailless males switch to an alternate reproductive tactic. No longer are they territorial, and they maintain overlaps with both males and females—not decrease overlaps as the tailed controls— as a consequence of tail loss.

Based on the smaller size of female home ranges in general, they overlap with very few males, and even fewer females. Females, regardless of tail condition, overlapped fewer neighbors at the end of the breeding season than the beginning. By the end of the season, females, due to small home range size and low initial overlaps, were essentially surrounded by a single territorial male lizard and were isolated from other females. This is exactly what Tinkle (1967) concluded in his seminal study of this species. For females, this may be the optimal strategy to maximize fitness.

The vegetative community provides valuable resources to the insectivorous *U. stansburiana*. Various plants provide shelter from predators and the elements, others provide an attractant for insects, and still others provide nesting sites. Therefore, the assumption is that individuals should secure territories that provide the most diverse assemblage of plants. Non-vegetative structures like rocks, dried cow chips, and debris add additional basking and refuging benefits. Initially, all lizards had equally diverse home range areas. Males that kept an intact tail throughout the breeding season increased the microhabitat diversity within their territories over time, to some extent by securing access to the rarer plant types or non-vegetative structures. This increased diversity came as these individuals were decreasing their home range size; however, diversity was not correlated with territory size. Tailless males increased the footprint of their home range without increasing their access to more diverse resources. In their case, having a large home range may actually be less than optimal with respect to microhabitat contents, but they expanded their home ranges to find and sneak females, not to garner better microhabitats. Home ranges of tailless males were dominated by large areas of open sand. Areas of open sand increase susceptibility to predators and overheating, and decrease access to prey items. Clearly this is not beneficial for the lizard, especially at this locality where midday temperatures can be lethal and lizards and their prey alike are not active in the open.

If as was suggested by Fox et al. (1990), tailless females signal lower social status and then occupy suboptimal areas, we should see a decrease in microhabitat diversity for tailless, treatment females and maintenance of diversity by tailed, control females. , The level of microhabitat diversity of tailless female home ranges were maintained, not decreased. And quite surprisingly, tailed females decreased the microhabitat diversity within their territories over the same time period. This result might be explained by late-season, enhanced use of one plant, the Havard Shin Oak. Tailed females increased the amount of shin oak within their territories over time at the cost of other plant types and non-vegetative structures, thereby lowering total microhabitat diversity. By the end of the breeding season for *U. stansburiana* in western Texas, the patchy shin oak thickets have formed a dense, almost impenetrable forest. The thickets form islands of shin oak, in the sea of open sand. At the base of these diminutive trees, large amounts of leaf litter accumulate. This area is optimal for nesting sites, and potentially the tailed females are preferentially defending the shin oak for access to the oak leaf litter for oviposition. This would lead to a decrease in microhabitat diversity within their territory. The tailless females maintained more diverse territories, but this may not represent the optimal strategy for reproductive female *U. stansburiana*. An interesting avenue to explore in the future is the effect nest substrate has on hatchling success. If nests in shin oak leaf litter have increased hatching success or produce larger hatchlings, then females should maximize the number of eggs deposited in the areas under the oaks and defend these areas more intensely.

The effects of autotomy on the distances moved between sightings were as predicted in the males. Tailless males moved longer distances, than their tailed counterparts. These tailless, treatment males also increased the distances of their movements over time; this was opposite of the pattern seen in tailed males. As the breeding season progressed, tailed (territorial) males moved shorter distances between sightings. This decrease is consistent with the constriction, or consolidation, of home range area that we observed for this group. Tailless (sneaker) males increased the distances they traveled probably in order to encounter more females and to avoid territorial males, as we predicted. Females did exactly as predicted; average distance traveled between sightings was not affected by tail status. Tailed and tailless females moved the same distances, and both groups shortened the distances moved over the course of the breeding season. This fits with females focusing on egg-laying and using the available resources for reproduction, not territory defense.

With respect to MDBO, males did not respond as predicted; regardless of tail status, males had equal MDBO in the Post-phase. Both tailed and tailless males showed a tendency to decrease MDBO from the Pre- to Post-phase, but these decreases were not statistically significant. The pattern in females, however, was as predicted. Tailed and tailless females decreased MDBO over time and had similar MDBO in the Post-phase. Tail status did not affect female MDBO. The overall decrease in MDBO for all lizards might reveal a temporal change in behavior toward the experimenter. One possible explanation is that the lizards may have become less wary of the experimenter as has been observed in this species and others over time as they habituate to human presence (Fox and Anderson, pers. obs.). Another possibility is that the experimenters became more efficient at sighting lizards over time. Both of these scenarios should affect the tail status groups similarly and would help explain why all groups decreased MDBO from the Pre- to Post-phase.

The costs of tail autotomy are clear in *U. stansburiana* and these plainly exert different burdens on the sexes. These costs are so great as to force males to give up territorial defense and assume an alternate tactic of sneaker. Tail autotomy as an antipredatory tactic is clearly beneficial to the individual—it often saves its life. However, the long-term costs associated with tail autotomy can lead to a cascade of changes in territorial and social behavior in *Uta stansburiana*. Most interesting is how these changes affect the sexes differently, and how the sexes then differentially deal with the handicap of losing the tail.

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Table 4.1: Morphology of all lizards at first capture (subjects and non-subjects). Measurements reported include: snout-to-vent length (SVL), tail length (TL), Natural Tail Break Length (NatTBL), head width (HW), and head length (HL). For NatTBL the mean ± 1 SD (mm), the sample size (n), and range (mm) are reported. For total number of sightings for all individuals the mean ± 1 SD (n) and the range (n) are reported. For all other measurements only mean ± 1 SD is reported.

Sex	**Year**	**Sample Size (n)**	**SVL (mm)**	**TL (mm)**	**SVL/TL ratio**	**NatTBL (mm; n; range)**	**HW (mm)**	**HL (mm)**	**Mass (g)**	**Total number of sightings (n; range)**
Male	**2008**	**87**	**50.31 ± 0.38**	**74.84 ± 2.38**	**1.47 ± 0.05**	**33.00 ± 3.31; 33; 9-74**	**9.71 ± 0.13**	**11.27 ± 0.14**	**4.36 ± 0.09**	**7.6 ± 0.83; 1-37**
	2009	**62**	**49.58 ± 0.48**	**78.22 ± 2.24**	**1.50 ± 0.06**	**39.61 ± 4.41; 23; 9-75**	**9.70 ± 0.15**	**10.03 ± 0.17**	**4.23 ± 0.13**	**7.85 ± 0.86; 1-26**
Female	**2008**	**101**	**46.51 ± 0.27**	**68.66 ± 1.69**	**1.48 ± 0.04**	**25.30 ± 3.47; 25; 3-66**	**8.49 ± 0.09**	**10.04 ± 0.10**	**3.43 ± 0.06**	**8.07 ± 0.70; 1-31**
	2009	**96**	**44.96 ± 0.31**	**68.01 ± 1.32**	**1.49 ± 0.04**	**28.11 ± 3.23; 28; 6-65**	**8.25 ± 0.09**	**8.29 ± 0.09**	**3.17 ± 0.73**	**8.59 ± 0.71; 1-28**

Table 4.2: Microhabitat Categories

Category	Name	Description
1	Open sand	Open sand, fully exposed
2	Shin oak	*Quercus havardii*; Havard Shin Oak found in large clumps or individual trees; root system acts to stabilize dunes, fully deciduous, large amount of associated leaf litter
3	Grass	Several species of “bunch grass,” forms impenetrable clumps which provide shelter from predators and heat
4	Yucca	*Yucca glauca*; long thin spines offer excellent protection from predators
5	Broomweed	*Amphiachryis dracuculoides*.; large flowering shrub, typically mushroom shape, provides an open, shaded, yet protected, area underneath
6	Mesquite	*Prosopis glandulosa*; largest plant on study area, growth is limited by ranch activities and conditions, thickets are very small (1-2 trees) and disjunct, provides excellent cover and often has an impenetrable packrat midden at base, these middens are used by lizards during the breeding season and as overwinter refuge
7	Rock/gravel	Exposed gravel, or caliche, used for road construction, sometimes larger rocks
8	Other plant	Any large bush, or shrub, not covered by Categories 2-6
9	Debris	Trash associated with ranching and oil activities (including exposed pipe, dried cow chips, boards, and mesquite stump piles from root plowing)

Table 4.3: Subject lizards (> 6 sightings) morphology during the Pre-phase. Independent sample t-tests were used to compare the years 2008 and 2009. Due to the non-significant differences in years, subsequent analyses pooled the years. All statistical tests are 2-tailed. Mean ± 1 SD.

Sex	**Year**	**Sample size (n)**	**SVL (mm)**	**t- score**	**p- value**	**TL (mm)**	**t- score**	**p- value**	**Mass (g)**	**t- score**	**p- value**	**Pre- sightings (n)**	**t- score**	**p- value**
Male	**2008**	**19**	**51.32 ± 4.10**	**1.246**	**0.220**	**80.08 ± 20.74**	**-0.520**	**0.606**	**4.34 ± 1.39**	**0.178**	**0.860**	**9.53 ± 3.20**	**-0.065**	**0.949**
	2009	**22**	**49.73 ± 4.05**			**82.89 ± 11.25**			**4.28 ± 0.93**			**9.59 ± 3.16**		
	Total	**41**	**50.46± 4.09**			**81.49 ± 16.51**			**4.31 ± 1.14**			**9.56 ± 3.13**		
Female	**2008**	**22**	**46.66 ± 2.90**	**2.009**	**0.053**	**67.02 ± 16.21**	**-0.523**	**0.603**	**3.27 ± 0.99**	**0.316**	**0.754**	**9.77 ± 3.42**	**1.025**	**0.312**
	2009	**32**	**44.63 ± 2.83**			**68.88 ± 11.50**			**3.15 ± 0.93**			**8.69 ± 2.49**		
	Total	**54**	**45.45 ± 3.00**			**68.21 ± 13.26**			**3.20 ± 0.95**			**9.13 ± 2.92**		

Table 4.4: Morphological comparison of the control and treatment groups (only surviving lizards are included, years are pooled). Measurements reported include: SVL, tail length at initial capture (Original TL), and the length of the tail remaining after experimentally induced autotomy (ExptTBL). All statistical tests are 2-tailed. Mean ± 1 SD.

Sex	Tail status	Sample Size (n)	SVL (mm)	t- score	p- value	Original TL (mm)	t- score	p- value		ExptTBL (mm)
Male	Control	10	50.70 ± 5.46	0.410	0.686	84.80 ± 13.19	0.304	0.763		0.90 ± 2.85
	Treatment	13	49.85 ± 4.54			85.96 ± 10.66				29.08 ± 6.86
Female	Control	13	46.57 ± 2.27	-1.164	0.254	72.15 ± 8.40	0.718	0.476		0.00 ± 0.00
	Treatment	18	44.77 ± 2.95			70.45 ± 8.74				23.62 ± 9.52

Table 4.5: Subject HR size (HR = Home Range or Territory; years pooled). Comparisons within groups (Pre vs. Post) made using the non-parametric Wilcoxon Matched-Pairs Signed-Ranks Test (1-tailed for treatment males, 2-tailed for all others). Mean ± 1 SD.

Sex	**Tail Status Group**	**Sample Size (n)**	**Pre- HR Size (m^2) ± 1 SD**	**Post- HR Size (m^2) ± 1 SD**	**Within Group Wilcoxon Z score**	**P- value**	**Total HR Size (m^2) ± 1 SD**
Male	**Control**	**10**	**425.14 ± 606.00**	**203.69 ± 155.79**	**-1.070**	**0.285**	**538.75 ± 208.17**
	Treatment	**12**	**476.29 ± 409.22**	**569.80 ± 831.11**	**-0.175**	**0.431**	**885.64 ± 282.45**
Female	**Control**	**13**	**239.23 ± 164.17**	**163.36 ± 199.30**	**-1.852**	**0.064**	**266.46 ± 35.34**
	Treatment	**18**	**229.56 ± 227.31**	**159.43 ± 96.67**	**-1.067**	**0.286**	**318.78 ± 60.96**

Table 4.6: Subject HR Overlaps (HR = Home Range or Territory; years pooled). Comparisons within groups (Pre vs. Post) made using the non-parametric Wilcoxon Matched-Pairs Signed-Ranks Test (2-tailed tests). Mean ± 1 SD.

			Same Sex Overlap (n)				**Opposite Sex Overlap (n)**			
Sex	**Tail Status Group**	**Sample Size (n)**	**Pre ± 1 SD**	**Post ± 1 SD**	**Within Group Wilcoxon Z score**	**p- value**	**Pre ± 1 SD**	**Post ± 1 SD**	**Within Group Wilcoxon Z score**	**P-value**
Male	**Control**	**10**	**2.20 ± 1.93**	**1.00 ± 0.81**	**-2.124**	**0.034**	**2.90 ± 1.72**	**1.20 ± 1.00**	**-2.254**	**0.024**
	Treatment	**12**	**2.31 ± 2.10**	**1.46 ± 1.12**	**-1.259**	**0.104**	**3.23 ± 3.09**	**2.00 ± 1.63**	**-1.743**	**0.081**
Female	**Control**	**13**	**1.46 ± 0.97**	**0.92 ± 0.86**	**-1.732**	**0.083**	**1.62 ± 1.39**	**0.92 ± 0.75**	**-1.642**	**0.101**
	Treatment	**18**	**1.83 ± 1.20**	**1.00 ± 0.97**	**-1.664**	**0.096**	**1.83 ± 1.40**	**1.22 ± 1.26**	**-1.231**	**0.218**

Table 4.7: Subject HR microhabitat diversity (H’, HR = Home Range or Territory; years pooled). Comparisons within groups (Pre vs. Post) made using the non-parametric Wilcoxon Matched-pairs Signed-Ranks Test (1-tailed for treatment males, 2-tailed for all others). Mean + 1 SD.

Sex	Tail Status	Sample Size (n)	Pre H’ ± SD	Post H’ ± SD	Mean Change in H’ within group	Within group Wilcoxon Z score	P- value
Male	**Control**	**10**	**1.25 ± 0.22**	**1.37 ± 0.17**	**0.101**	**-1.988**	**0.047**
	Treatment	**12**	**1.28 ± 0.24**	**1.17 ± 0.21**	**-0.067**	**-1.363**	**0.087**
Female	**Control**	**13**	**1.21 ± 0.20**	**0.96 ± 0.46**	**-0.252**	**-2.040**	**0.041**
	Treatment	**18**	**1.37 ± 0.22**	**1.19 ± 0.20**	**-0.098**	**-1.023**	**0.306**

Table 4.8: Distance moved between sightings and mean days between observations (MDBO); years pooled. Comparisons within groups (Pre vs. Post) made using the non-parametric Wilcoxon Matched-Pairs Signed-Ranks Test. Mean ± 1 SD.

Sex	**Tail Status Group**	**Sample Size (n)**	**Pre-Distance (m)**	**Post-Distance (m)**	**Mean Change in distance moved m)**	**Within Group Wilcoxon Z-score**	**p value**	**Pre-MDBO (d)**	**Post-MDBO (d)**	**Within Group Wilcoxon Z-score**	**p value**
Male	**Control**	**10**	**15.45 ± 13.70**	**10.65 ± 5.37**	**-4.80**	**-0.764**	**0.445**	**3.30 ± 1.17**	**2.27 ± 1.00**	**-1.886**	**0.059**
	Treatment	**12**	**16.39 ± 6.20**	**19.41 ± 14.14**	**+3.02**	**-0.804**	**0.211**[1]	**2.96 ± 1.25**	**2.25 ± 0.53**	**-1.915**	**0.056**
Female	**Control**	**13**	**12.05 ± 4.32**	**11.18 ± 9.51**	**-0.87**	**-1.363**	**0.173**	**3.46 ± 2.07**	**2.46 ± 1.05**	**-1.664**	**0.096**
	Treatment	**18**	**11.41 ± 5.25**	**10.24 ± 3.22**	**-1.17**	**-0.806**	**0.420**	**3.77 ± 1.38**	**2.42 ± 0.86**	**-2.675**	**0.007**

[1] 1-tailed t-test

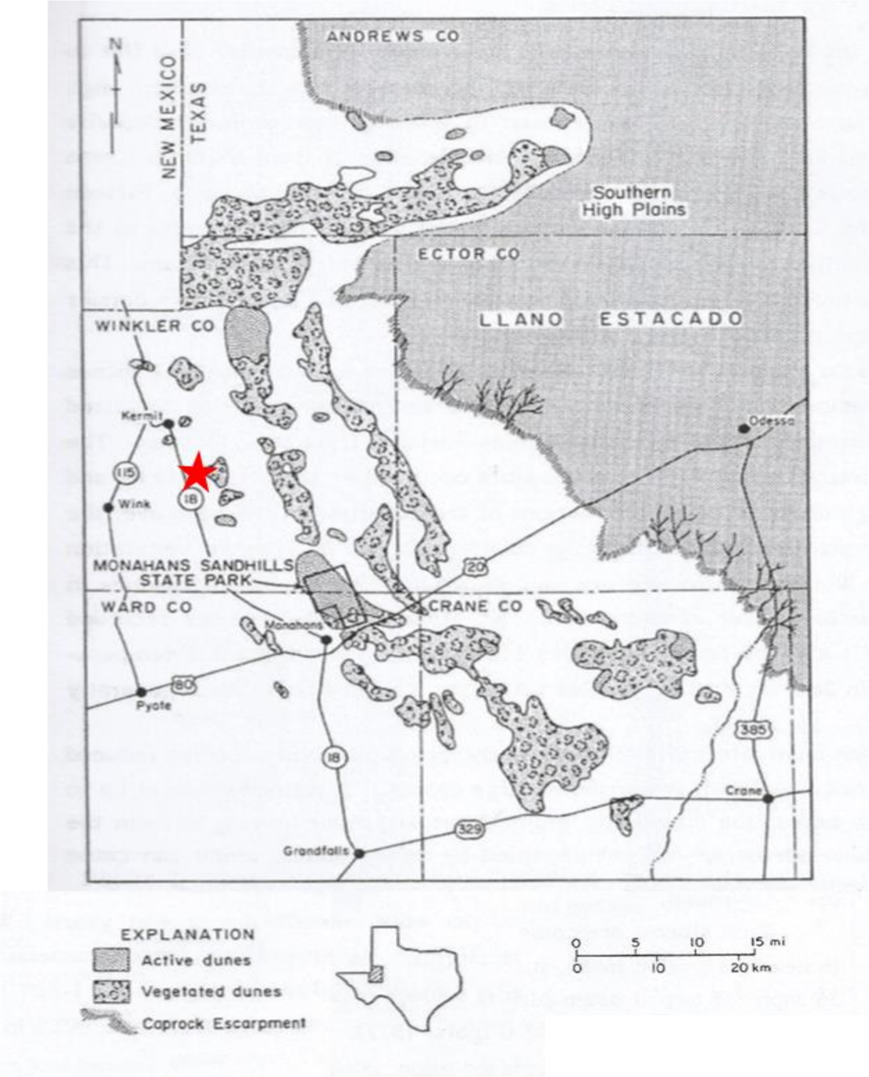

Figure 4.1: Map representing western Texas and the study region. The red star denotes approximate location of study site. Modified from Machenberg 1984.

Figure 4.2: Aerial photograph of the study site. Red lines represent boundaries of the study plot. The study area was bounded on the west by a gravel roadbed used to service the oil and natural gas machinery. The northern edge was a barbed wire fence. The eastern edge was delimited by a cleared easement above an underground pipeline used to transport oil and natural gas. The southern boundary was a line roughly parallel to the northern edge; this line was demarcated by flags placed at 20 m intervals.

<table>
<tr><td colspan="2" rowspan="5">All lizards (intact tails or natural breaks)</td><td>< 6 sightings</td><td colspan="3">Non-subjects</td></tr>
<tr><td rowspan="4">> 6 sightings</td><td rowspan="4">Subjects</td><td rowspan="2">Control (intact tail)</td><td>Survivors</td></tr>
<tr><td>Non-survivors</td></tr>
<tr><td rowspan="2">Treatment (autotomy induced)</td><td>Survivors</td></tr>
<tr><td>Non-survivors</td></tr>
<tr><td colspan="3">Pre-Phase</td><td colspan="3">Post-Phase</td></tr>
<tr><td>Week 0</td><td>→ → →</td><td>Week 6</td><td colspan="2">→ → →</td><td>Week 12</td></tr>
<tr><td colspan="2"></td><td>Pre-MCP demarcated and micro-habitat H’ measured</td><td colspan="2"></td><td>Post-MCP demarcated and micro-habitat H’ measured</td></tr>
</table>

Figure 4.3: Graphic timeline depicting the field season and major events for the groups of lizards.

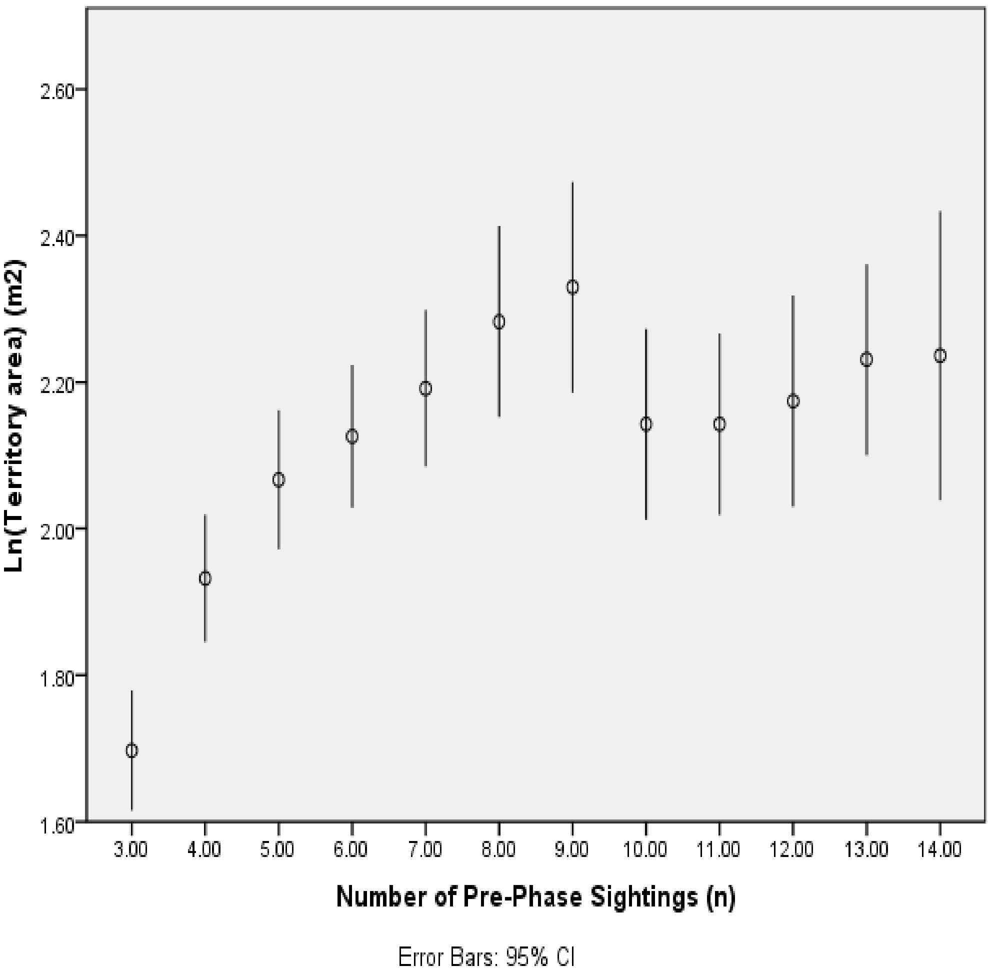

Figure 4.4: Relationship between number of sightings and ln home range size during Pre-phase based on the 95% MCP for resident *Uta stansburiana*. Subsequent analyses included only individuals with six or more sightings.

VITA

Matthew Lee Anderson

Candidate for the Degree of

Doctor of Philosophy

Thesis: THE EFFECT OF TAIL LOSS ON SPRINT SPEED, MATING STRATEGIES, AND TERRITORY SIZE AND QUALITY IN THE LIZARD *UTA STANSBURIANA*

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Herpetologists’ League, 2007- Present
Southwestern Association of Naturalists, 2007- Present

Name: Matthew L. Anderson Date of Degree: May, 2013

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: THE EFFECT OF TAIL LOSS ON SPRINT SPEED, MATING STRATEGIES, AND TERRITORY SIZE AND QUALITY IN THE LIZARD *UTA STANSBURIANA*

Pages in Study: 115 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: The study was primarily a field based effort to monitor and document changes in the behavior, mating strategies, and territory size and quality of a population of the lizard *Uta stansburiana* following tail autotomy. The study had three objectives, to determine if tail loss: 1. reduces sprint performance in one or both sexes of *U. stansburiana* and if so how one or both sexes might compensate, 2. changes behavior of either sex in the field (focusing on territorial aggression, mating strategies, and foraging rate), and 3. leads to decreases in survivorship, territory size, or territory quality (measured by assessing territorial overlaps, microhabitat diversity, distance moved between sightings, and days between sightings).

Findings and Conclusions: I documented changes in sprint performance, territorial and foraging behavior, territory size and quality, movements, and mating strategies in the lizard *Uta stansburiana* following tail autotomy. This species is sexually dimorphic and the effects of autotomy are clearly different between the sexes. Males showed a clear compensatory effort to maintain sprint performance following tail loss, whereas females did not. Males responded to intruders into their territories more aggressively than females, but tail loss did not affect aggression in either sex. Males attacked real tethered intruders more aggressively than mirror-image intruders, regardless of tail status. Focal observations were used to uncover subtle differences in behavior between tailed and tailless individuals. Tailless males behaved less conspicuously than tailed males. Tailless females increased foraging rate, potentially offsetting the burdens of tail regeneration during the energetically demanding reproductive season. However, this increased foraging did not lead to increased fecal production in tailless females. Tail loss negatively impacted survivorship in both sexes. When looking at territory quality, tailless males displayed a pattern consistent with a switch from territoriality to a sneaker strategy, i.e., they moved greater distances, expanded their home range and maintained multiple overlaps with females, while not defending rare microhabitats. Post-autotomy females signaled lowered social status with the lack of their tail, fought less, and made the best of a bad situation. As predicted, tail loss did not alter female territory size or overlaps. Overall, clear sexual differences in the strategies of *U. stansburiana* following tail autotomy were observed. By addressing a single adaptation, tail autotomy, and examining its costs, this study elucidated the sexually disparate effects of tail autotomy on life-history, territoriality, behavior, and mating strategy in *U. stansburiana*.

ADVISER’S APPROVAL: Stanley F. Fox