**Boldness does not influence the territorial dynamics of
the ornate tree lizard (*Urosaurus ornatus*)**

EVS4009 Honours Research Project

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Abstract

In environments characterised by heterogeneous resource distribution, the ideal despotic distribution predicts that dominance can affect habitat settlement patterns. Although dominance has often been shown to be a fundamental driver of territorial dynamics, other behaviours such as boldness may also be important. I tested the hypothesis that variation in boldness within populations of ornate tree lizards *Urosaurus ornatus* dictates territorial dynamics. Bolder individuals should take more risks to exploit resource rich environments and, thus, they should occupy the highest quality habitats. I quantified boldness of tree lizards in two habitats (wash and upland), that differ in thermal quality and in food abundance, by calculating the time it took to capture lizards. Boldness did not differ between habitats, but females became bolder while males became shyer as the active season progressed. Thus, boldness may not contribute to the territorial dynamics of *U. ornatues*. To my knowledge, this is the first study to assess the influence of *U. ornatues* boldness on its territorial dynamics in a natural setting.

Key words: Boldness, territorial dynamics, *Urosaurus ornatus*, behaviour

Introduction

The ideal free distribution theory first formally termed by Fretwell and Lucas (1970), assumes that all individuals are equally "free" to occupy any space within a given habitat (Calsbeek and Sinervo 2002). However, in environments characterised by heterogeneous resource distribution, the ideal despotic distribution predicts that dominance can affect habitat settlement patterns of residing populations (Paterson and Blouin-Demers 2017). For example, in territorial species, differences in social dominance among individuals generate competitive asymmetries (Taylor and Lattanzio 2017). These variations in behaviour create an ideal despotic territorial distribution, wherein dominant individuals secure the highest quality habitats while forcing subordinates into less favourable habitats (Calsbeek and Sinervo 2002).

Within an environment, the quality of a specific habitat depends on multiple factors, for example food abundance, nest site quality and environmental conditions (Fretwell and Lucas 1969). For ectotherms, the fitness benefits of settling in a specific habitat often depends heavily on the environmental temperature (Blouin-Demers and Weatherhead 2001; Hughes and Grand 2000) because regulation of optimal body temperatures (T_o) is dependent on the habitat thermal quality. High thermal quality habitats are characterized as habitats with operative environmental temperatures (T_e) close to the species' preferred body temperatures (T_{set}) (Paterson and Blouin-Demers 2018). Variations in this important abiotic characteristic creates a heterogeneous environment which can affect habitat settlement patterns (Blouin-Demers and Weatherhead 2001).

Although dominance has often been shown to be a fundamental driver of territorial dynamics in heterogeneous environments (Calsbeek and Sinervo, 2002), other behaviours such as boldness should also contribute to the process (Taylor and Lattanzio 2017). Boldness can be defined as an individual's tendency to resist escape under the perceived threat of a predator (Taylor

47   and Lattanzio 2016). A bold individual will be more likely to resist fleeing, while a shy individual

48   will tend to flee (López et *al.* 2005). This behaviour has received increased attention in the last

49   decade (St Clair et *al.* 2016; Highcock and Carter 2014; Ward-Fear et *al.* 2018) due to its broad

50   implication for social interactions, predator-prey dynamics, as well as the ecological dynamics of

51   entire populations (Taylor and Lattanzio 2016). Recent studies have shown that boldness is

52   consistent among individuals, both through time and over varying situations (Kashon and Carlson

53   2017; Highcock and Carter 2014), which suggests that it is a "personality trait". Consistency in

54   behaviour among individuals, and differences in behaviour between individuals can result in

55   variations in fitness (Cote et *al.* 2008).

56   The three most common methods used to quantify boldness in lizards are: 1) "flight

57   initiation distance", 2) "flight distance" and 3) "time in refuge" (Cooper 2009). By simulating an

58   approaching predator, a researcher can force a lizard to escape or seek refuge. Measuring the

59   distance between the researcher and the initial lizard location before it fled or the time the lizard

60   spends in refuge provide proxies for boldness. Measurements of the flight distance, how far a lizard

61   flees from its initial location, is an alternative method. It is important to note that although humans

62   are not a natural predator to lizards, there are no known qualitative differences in escape behaviour

63   between an approaching researcher and a predator (Cooper 2009).

64   Boldness has considerable implications on an individual's life history because bold

65   individual will be able to maximize opportunities to acquire essential resources, such as food, and

66   to establish and defend its' territory despite the risk of predation (Taylor and Lattanzio 2016). For

67   example, Seltmann et *al.* (2013) found an asymmetry in the nest-site selection of eider ducks

68   (*Somateria mollissima*) resulting from variation in boldness. Bold female ducks selected higher

69   quality, concealed nests further away from the coast at the expense of increased mortality by

70   predation. This suggests that bolder individuals benefit from acquiring the highest quality habitats

71   despite the risk of predation. Although the acquisition of resources is important, there are

72   associated trade-offs to exhibiting bold behaviours, such as increased exposure to predators

73   (Hulthén et *al*. 2017). Being bold can lead to access to higher quality habitats (Bonnot et *al*. 2018,

74   Seltmann et *al*. 2013), however bold individuals may be at a risk to increased predation while

75   acquiring resources. In contrast shy individuals may decrease their exposure to predators but as a

76   result, they may not gain access to the best quality habitats (Bonnot et *al*. 2018).

77   In addition, bolder individuals may also occupy higher quality habitats because boldness

78   is often linked to social dominance hierarchies (Dahlbom et *al.* 2011; Pottinger 2001; Sundström

79   et *al.* 2004). Boldness is closely related to social status as bolder individuals have been documented

80   to be more aggressive and are ultimately more dominant (Dahlbom et *al.* 2011). Dahlbom et *al.*

81   (2011) suggested that boldness and social dominance may even have a common genetic basis.

82   Further, individuals that have a larger body size are known to be more dominant and may also be

83   bolder (Harris et *al.* 2010; Kohlsdorf et *al.* 2006; Stamps 1984). Larger head sizes, specifically,

84   have previously been linked to higher dominance (Gvozdik and Van Damme 2003) and boldness

85   (López et *al.* 2005). Social dominance has also been observed in species exhibiting colour

86   polymorphism, wherein a dominant morph secures the habitat of highest quality (Healy 2008).

87   Predator escape observations of colour polymorphic tawny dragon lizard (*Ctenophorus decresii*)

88   have found that aggressive colour morphs are bolder (Yewers et *al.* 2016). As dominant individuals

89   have often been shown to express bolder behaviours (Dahlbom et *al.* 2011; Pottinger 2001;

90   Sundström et *al.* 2004), habitat settlement patterns resulting from hierarchal dominance may also

91   be observed in the context of boldness.

92   In order to assess the potential link between habitat quality and boldness I used ten

93   populations of ornate tree lizards (_Urosaurus ornatus_) living in two habitat types that differ in

94   quality. The ornate tree lizard is one of Arizona's most widespread lizards living in a variety of

95   habitats including dry stream beds, forests, and talus slopes (Brennan and Holycross 2006). This

96   species displays various colour morphs which are associated with differences in behavioural traits

97   (Paterson and Blouin-Demers 2017), which are linked to asymmetries in social dominance

98   (Thompson and Moore 1991). In this species, the dominant blue-throated males have been

99   documented to occupy the higher quality habitats (Taylor and Lattanzio 2016). Furthermore, the

100   ornate tree lizard is a territorial species, defending its habitat to exploit its resources, such as mates

101   (M'Closkey et _al._ 1987). Thus, habitat settlement patterns resulting from territorial competitions

102   between morphs generates an ideal despotic distribution, wherein dominant individuals

103   monopolize the best habitat (Calsbeek and Sinervo 2002; Taylor and Lattanzio 2016).

104   Although the implications of polymorphism and dominance of the ornate tree lizard on

105   social interactions and settlement patterns have been well studied, to my knowledge, only one

106   study has evaluated the influence boldness behaviours on the territorial dynamics of the ornate tree

107   lizard (Taylor and Lattanzio 2016). This study found variations in boldness between individuals

108   and suggested important implications of this behaviour on territorial interactions. However, these

109   conclusions were based on an in vitro experiment which may not reflect the true natural variations

110   within the population (Carter et _al._ 2012). As a result, it is uncertain whether boldness influences

111   the habitat settlement pattern of the ornate tree lizard in a natural setting. However, as bolder

112   individuals are more dominant (Dahlbom et _al._ 2011; Pottinger 2001; Sundström et _al._ 2004) and

113   are more willing to take risks to exploit resource rich environments (Bonnot and _al._ 2018; Seltmann

114   et _al._ 2013), I hypothesize that variation in boldness within populations of ornate tree lizards

115   dictates territorial dynamics. I predict that ornate tree lizards occupying the higher quality habitat

116   will be bolder than lizards living in the lower quality habitat.

Methods

Study site

119   From 01 May to 24 July 2018 I studied the boldness of the ornate tree lizards (*Urosaurus*

120   *ornatus*) at ten sites in the Chiricahua Mountains which is part of the Coronado National Forest

121   located in southeastern Arizona, USA. (Figure 1). Each site extended 300 m down a dry, rocky

122   stream bed with open canopy cover (wash) and 50 m into the adjacent forested habitat with closed

123   canopy cover (upland) (Figure 2).

124
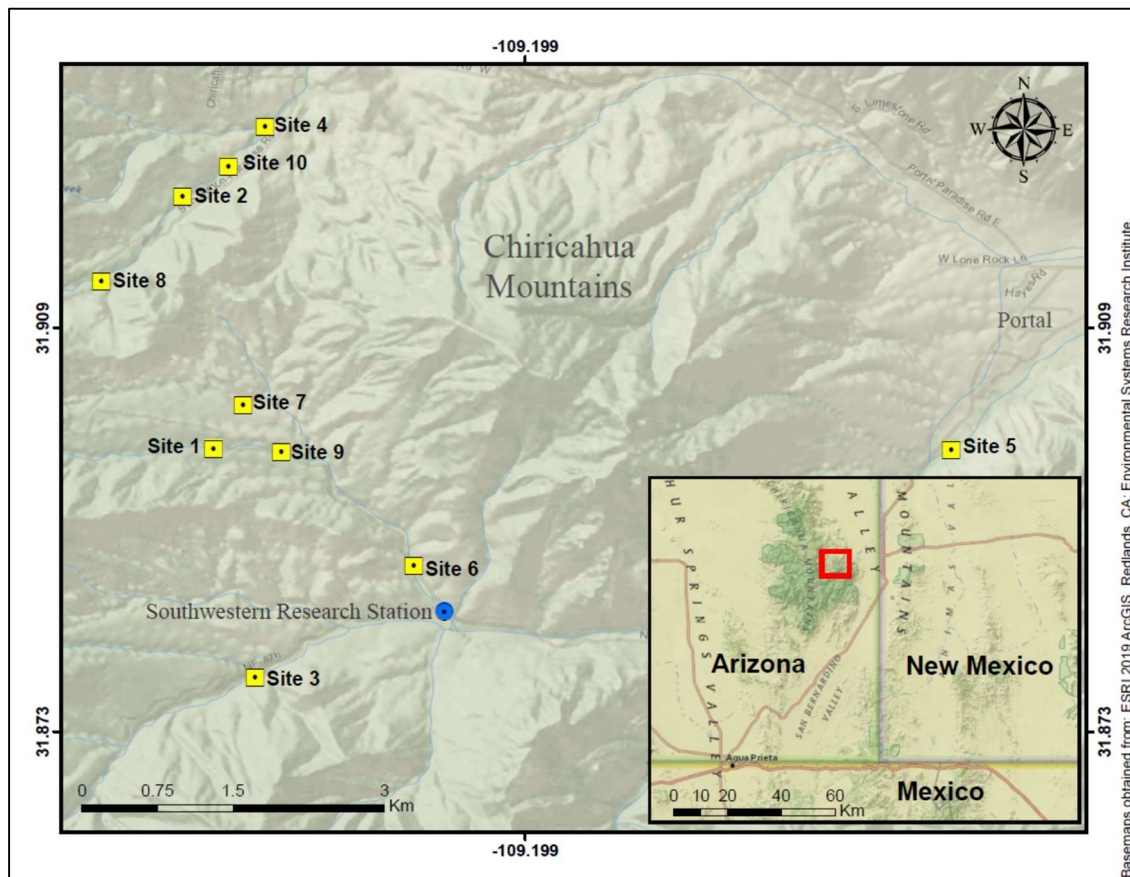
Figure 1. Locations of the 10 sites used during the 2018 field season to capture *Urosaurus ornatus* in the Coronado National Forest, Chiricahua Mountains, southeastern Arizona, USA. Projected Coordinate System: World WGS 1984. See table in annex for complete list of UTM coordinates.

129
130 **Figure 2.** Photograph take at site 4, illustrating the opened canopy wash habitat (left) and the
131 closed canopy upland habitat (right) within the Chiricahua Mountains, Arizona, USA.
132

Thermal quality

134　　To determine operative environmental temperatures (T_e), I placed iButton temperature

135 loggers, painted brown to reflect the thermal properties of the ornate tree lizard, randomly

136 throughout the various surface microhabitats (on a log, on a rock, and on a tree) available in both

137 the wash and upland (Herczeg et *al*. 2006, Paterson and Blouin-Demers, 2018). Because lizard

138 activity such as foraging, guarding territories and mating is limited by environmental temperatures

139 at the surface (not inside refuges), the microhabitats sampled represented common perching areas

140 of lizards in each habitat. I assumed that lizards were always able to seek refuge from hot surface

141 temperatures in the numerous hiding locations available (under bark, under leaf litter, under rocks,

142 under logs, etc.) and so what limits lizard activity is the surface T_e. In my observations where perch

143   location was noted (n = 1101), 98% of lizards perched on trees, logs or rocks, so I assumed these

144   microhabitats accurately represent the microhabitats used by tree lizards in the wash and upland

145   habitats.

146   I determined the thermal quality of the wash and upland habitats at each site by comparing

147   the range of T_e to the preferred temperature range of the species (T_{set}; 32.2°C to 36.0°C) which

148   was previously determined by Paterson and Blouin-Demers (2018) using a laboratory thermal

149   gradient in the absence of any ecological costs. Specifically, thermal quality was measured as the

150   proportion of the day where T_e reached T_{set} in each habitat.

151   **Boldness**

152   In order to assess boldness, I used a digital watch to measure the time it took to capture

153   lizards with a rod and noose. Although a novel approach, time to capture (TTC) should be an

154   appropriate proxy for boldness as a bolder individual should take less time to catch. This is due to

155   their tendency to resist escape (Highcock and Carter 2014), have shorter flight initiation distances

156   and overall flight distances (Cooper 2009), as well as taking less time to emerge from refuge

157   (López et *al.* 2005; Sneddon 2003). These combined measures influence the TTC as researchers

158   delegated less time to chase, wait and capture bold lizards.

159   Capture sessions consisted of walking throughout the site while delegating search times

160   evenly between the two habitats. Once located, the researchers approached the lizards at a

161   consistent speed, standardizing the approach and thus, minimizing any bias (Cooper 2009). The

162   timer was initiated when the lizard fled its' perch and stopped once the lizard was captured.

163   However, if the lizard did not flee within approximately 3 metres of distance, the researcher started

164   the timer and attempted to capture it. When captured, lizards were placed in a uniquely numbered

165 cotton bag and kept in a shaded area until processing. Each capture location was recorded with a

166 handheld GPS unit to ensure that the lizards were returned to their location of capture.
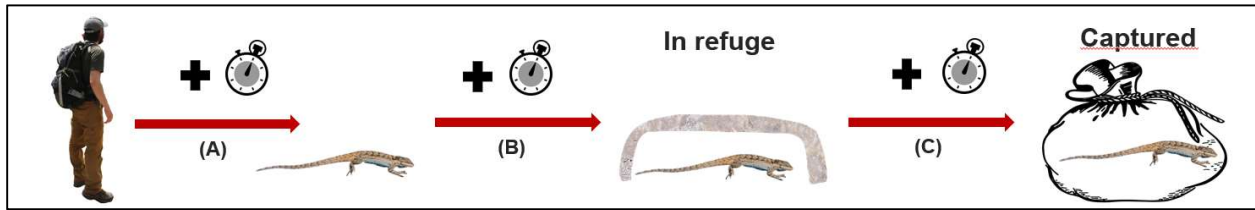
167
168 **Figure 3.** A schematic of time to capture (TTC) measurements of lizards as a function of (A) flight
169 initiation distance, (B) flight distance and (C) the time in refuge.
170

Morphology

172   During processing, snout-vent-length (SVL; ± 0.1 mm) and head length (tip of the snout to

173 the posterior edge of the dentary (angular); ± 0.1 mm) was measured with digital callipers.
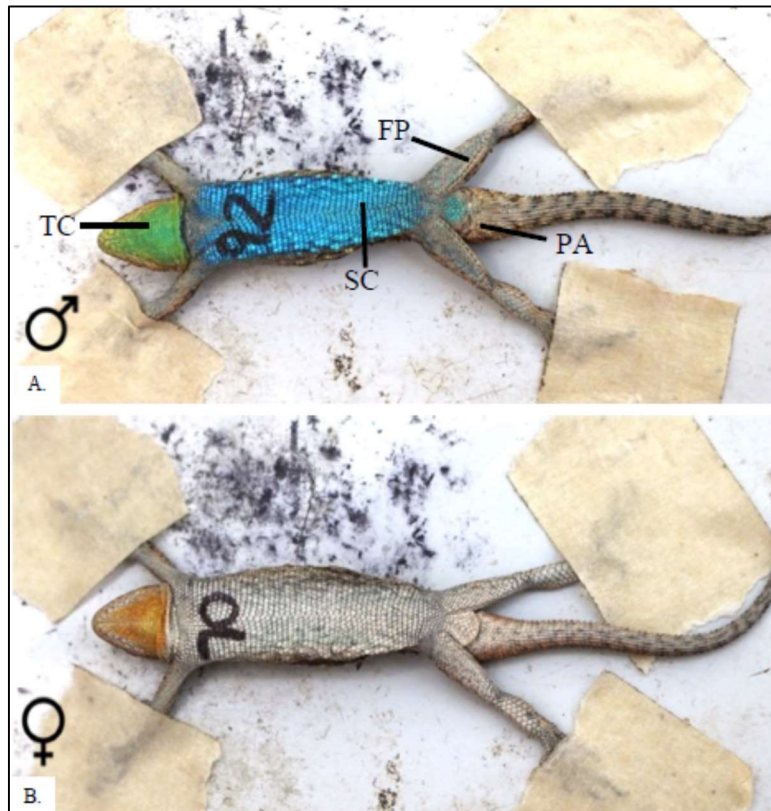
174 **Figure 4.** Picture of the ventral side of a male (A) and female (B) *Urosaurus ornatus* during
175 processing. Males were identified by their enlarged post-anal scales (PA), enlarged femoral pores
176 (FP), stomach colouration (SC) and throat colouration (TC). Figure reproduced with permission
177 from A. Lymburner.
178

179   Lizards were sexed by the presence (males) or absence (females) of enlarged post-anal

180 scales (Delaney and Warner, 2016), enlarged femoral pores, stomach colouration and throat

181 colouration (Figure 4). Lizards were then marked non-permanently on their stomach and head with

182 a unique number using a felt tip marker. These numbers remained visible for approximately two

183 weeks (depending on lizard shed cycle) and allowed for repeated measures.

184 **Statistical analyses**

185   All statistical analyses were completed using R (R Core Team, 2018). A two-sided t-test

186 ($\alpha = 0.05$) was used to determine the differences in boldness of lizards between the wash and

187 upland habitats (function 't.test'). To respect model application assumptions, the log of TTC was

188 used as the dependent variable to normalize residuals (Figure 5).

189   Additionally, a generalized linear mixed-effects model (package 'lme4', function 'lmer')

190 was used to determine the variables that affect lizard boldness. Habitat, the variable of interest,

191 was included as fixed effect. Other important variables that may affect boldness were included in

192 my model as controls: Sex (Chantina et *al.* 2009), head length (HL) (López et *al.* 2005), snout-

193 vent-length (SVL) (Harris et *al.* 2018) and date were included as a fixed effect. Because date, HL

194 and SVL were on very different scales, all three variables were standardized using the function

195 'scale'. Since three researchers collected the data, "researcher ID" was added as a random effect.

196 Likewise, to control for any effects of repeated captures of individuals, the number of captures

197 (e.g. first capture = 1, second capture = 2) was added as a random effect (CP). To control site or

198 individual effects, lizard identification (ID) nested within site was also included as a random effect.

199 The log of TTC was used as the dependent variable to normalize residuals.

200   To evaluate fitting of simplified TTC models, simplified models were compared with a

201 backwards stepwise analysis using Akaike's information criterion (AIC). I eliminated non-

202 significant effects (α > 0.05) to produce a final simplified model with only significant effects

203 (Table 1). The most parsimonious model (i.e. lowest AIC value) was selected as the final model.

204 Conditional R^2 values for each simplified model were compared (package 'MnMIn', function

205 'r.squaredGLMM') to insure that elimination of variables did not reduce model fitting.

Results

207   Pooling all sites, in the wash, I captured 357 lizards 556 times, and in the upland, I caught

208 469 lizards 694 times. I captured 430 females 616 times and 391 males 629 times (total n =1250).

209 Thermal quality

210   Lymburner (unpublished data 2019) found that the thermal quality was significantly

211 higher in the wash than the upland habitat (Figure 5). There was a higher proportion of the day

212 where (T_e) was within T_{set} (32.2 to 3.0°C) in the wash habitat.
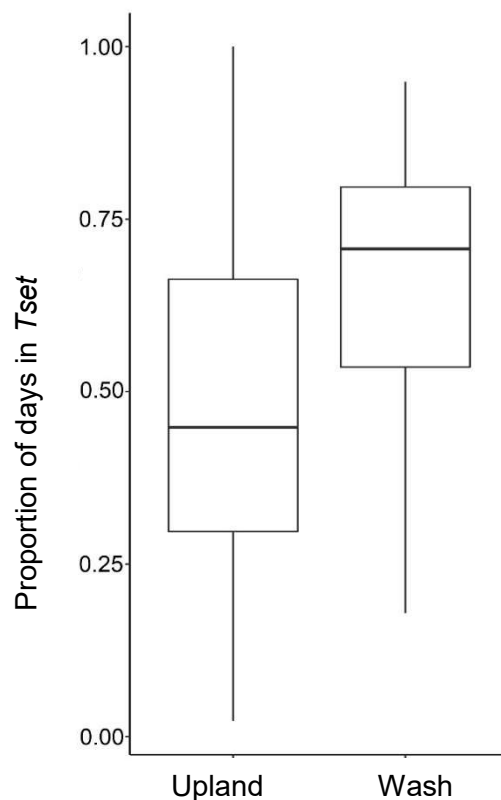
213
214 **Figure 5.** Boxplot of the proportion of the day where T_e was within T_{set} the upland and the wash
215 habitats. Figure reproduced with permission from A. Lymburner.

216   **Time to capture**

217   TTC did not significantly differ between the wash and the upland habitats (t = -0.20, df =

218   1250, p = 0.84). The average and median TTC in the wash habitats was 3.64 min and 1.69 min,

219   respectively.
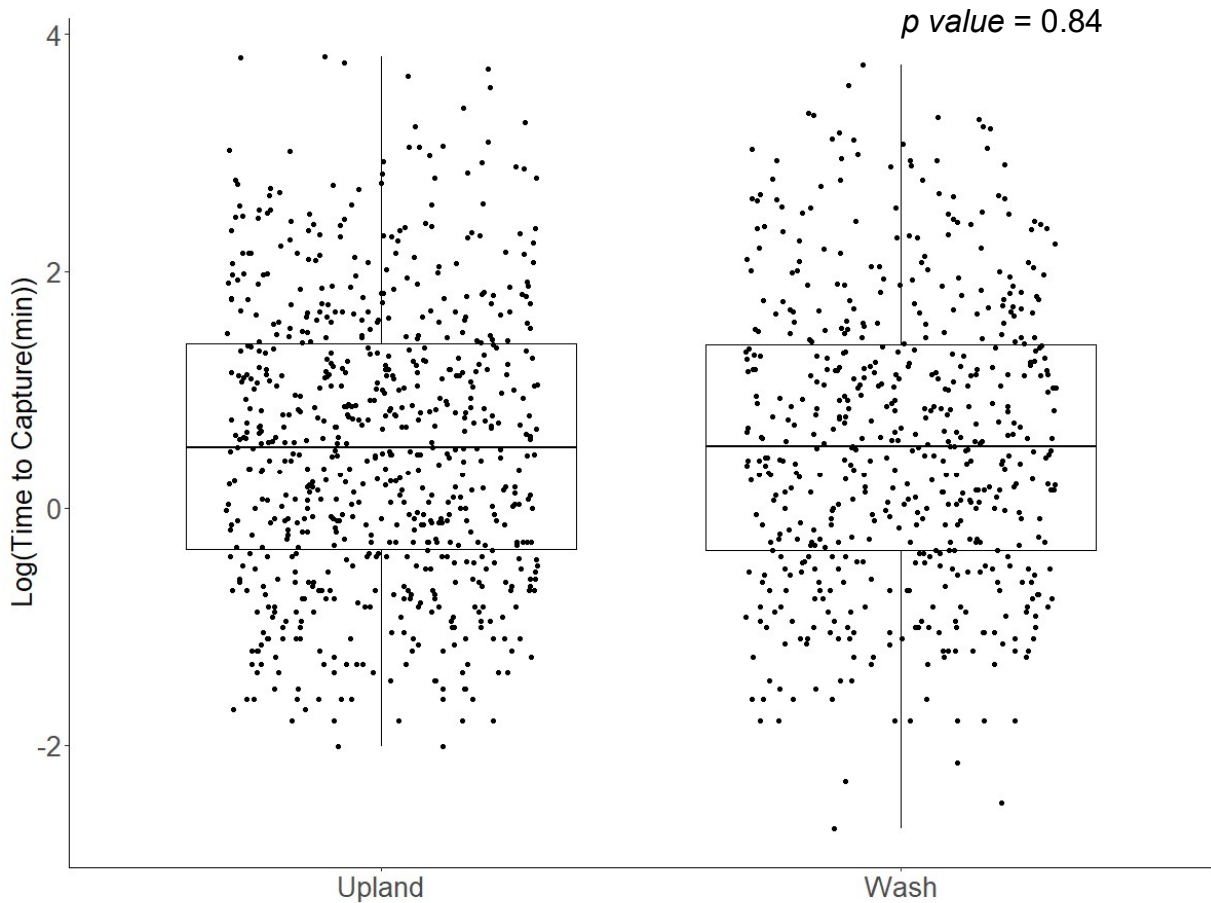
220   **Figure 6.** Boxplot of the logarithm of time to capture in minutes of *Urosaurus ornatus* in the
221   upland and wash habitats.
222

223   The average and median TTC in the upland habitats was 3.57 min and 1.68 min,

224   respectively. Pooling all sites and habitats, the average and median time to capture was 3.60

225   minutes and 1.68 minutes, respectively (Figure 6).

226   Following the backwards stepwise AIC analysis (Table 1), the simplified model (Figure

227   7) was the most parsimonious model describing boldness in the ornate tree lizard (AIC =

228   3894.543). This model included sex ($p = 0.51$), date ($p < 0.01$) and the interactions between these

229   variables ($p = 0.02$). This model explained 22% of the variation of boldness (R^2 value $= 0.22$). The

230   random variables remained in the model for control purposes. Removing the random variables

231   significantly changed the model and reduced the conditional R^2 value.   TTC did not differ

232   with SVL ($\chi^2 = 0.2097$, df $= 1$, p $= 0.65$), nor between sexes ($\chi^2 = 0.6764$, df $= 1$, p $= 0.41$), but did

233   increase with date ($\chi^2 = 10.9609$, df $= 1$, p < 0.01). Additionally, there was a significant interaction

234   between sex and date ($\chi^2 = 4.3721$, df $= 1$, p $= 0.04$).

235
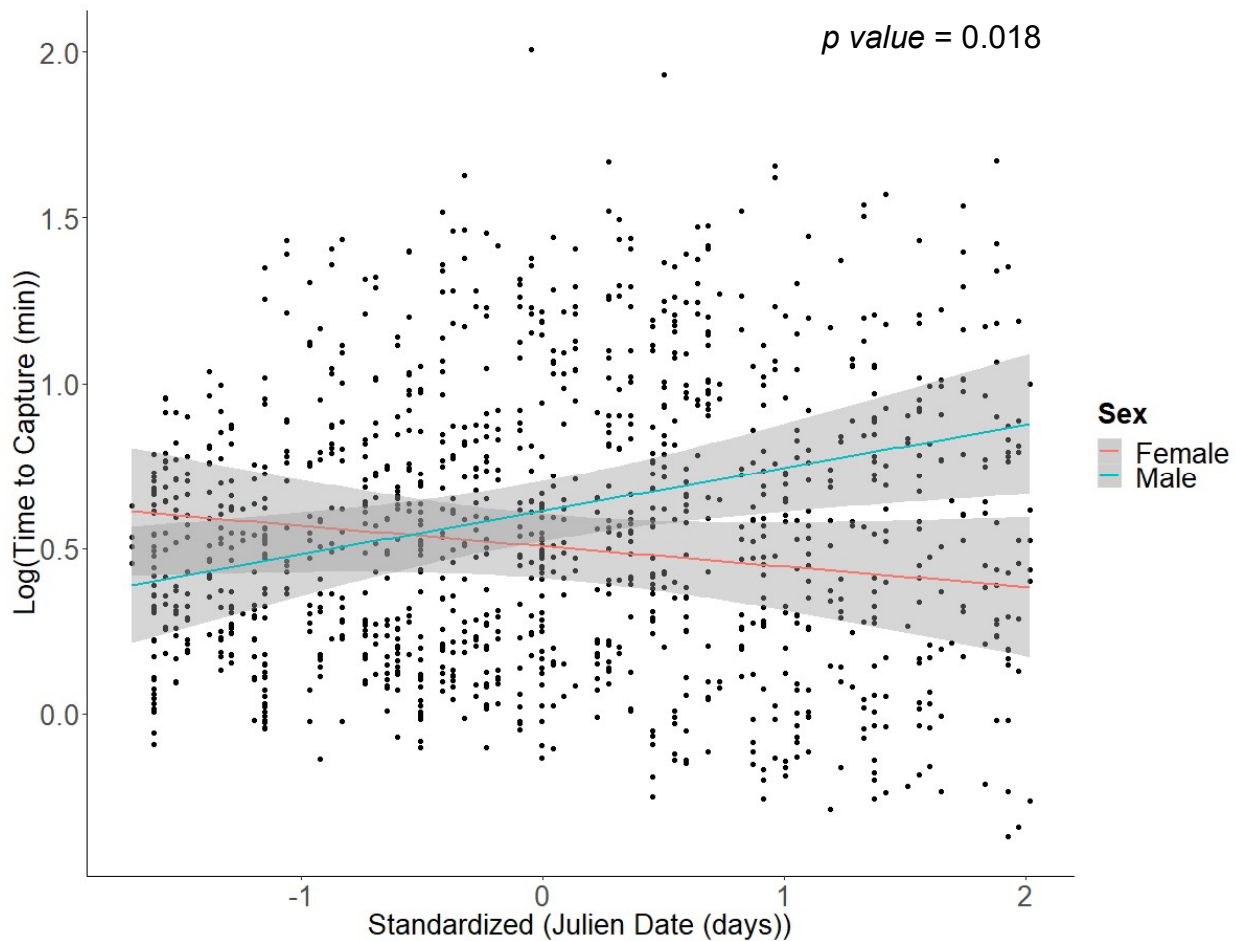
236   **Figure 7.** The predicted values of logarithm of time to capture as a function of the standardized
237   Julian date for male and female lizards. The grey shading represents the 95% confidence interval
238   of the blue (male) or red (female) regression lines.

14

Table 1. Conditional R^2 and AIC values for fitted models of time to capture following VIF analysis. I chose the most parsimonious model to explain lizard's boldness (model 10).

Model		Conditional R^2	AIC
1	TTC)~Habitat+Sex+SVL.z+Date.z+Habitat:Sex+Habitat:SVL.z+Sex:SVL.z+Sex:Date.z+SVL.z:Date.z+Habitat:Sex:SVL.z+Sex:SVL.z:Date.z*(1|Researcher)*(1|CP)*(1|Site/ID), data = Bold)	0.2191	3935.913
2	TTC~Habitat+Sex+SVL+Date+Habitat*Sex+Habitat*SVL+Sex*SVL+Sex*Date+SVL*Date+Habitat*Sex*SVL+Sex*SVL*Date +(1|Researcher)*(1|CP)*(1|Site/ID)	0.2191	3930.387
3	TTC~Habitat+Sex+SVL+Date+Habitat*Sex+Habitat*SVL+Sex*SVL+Sex*Date+Habitat*Sex*SVL+Sex*SVL*Date +(1|Researcher)*(1|CP)*(1|Site/ID)	0.2191	3930.387
4	TTC~Habitat+Sex+SVL+Date+Habitat*Sex+Habitat*SVL+Sex*SVL+Sex*Date+Sex*SVL*Date +(1|Researcher)*(1|CP)*(1|Site/ID)	0.2184	3927.699
5	TTC~Habitat+Sex+SVL+Date+Habitat*Sex+Habitat*SVL+Sex*SVL+Sex*Date+(1|Researcher)* (1|CP)*(1|Site/ID)	0.2210	3918.692
6	TTC~Habitat+Sex+SVL+Date+Habitat*Sex+Habitat*SVL+Sex*Date+(1|Researcher)*(1|CP)*(1|Site/ID)	0.2195	3913.849
7	TTC~Habitat+Sex+SVL+Date+Habitat*Sex+Sex*Date+(1|Researcher)*(1|CP)*(1|Site/ID)	0.2204	3909.607
8	TTC~Habitat+Sex+SVL+Date+Sex*Date+(1|Researcher)*(1|CP)*(1|Site/ID)	0.2215	3906.071
9	TTC~Sex+SVL+Date+Sex*Date+(1|Researcher)*(1|CP)*(1|Site/ID)	0.2211	3900.565
10	**TTC~Sex+Date+Sex*Date+(1|Researcher)*(1|CP)*(1|Site/ID)**	**0.2224**	**3894.543**

* Represents an interaction between 2 variables, ( ) represent random variables

Discussion

Lizard habitat selection can be structured by consistent behavioural differences between individuals (Paterson and Blouin-Demers 2017). I tested whether variations in individual boldness within populations of ornate tree lizards would dictate territorial dynamics. The thermal quality of the upland and wash did differ significantly (Lymburner unpublished data 2019) however, I did not find variations in the spatial distribution of boldness. These results do not support the hypothesis that variations in boldness dictates territorial dynamics, which would have resulted in an asymmetry in the spatial distribution of this behaviour. Contrary to my prediction, there was no significant difference in ornate tree lizard boldness between the upland and the wash habitats. Although habitat was not a significant predictor of boldness (measured as time it took to capture a lizard), the final model revealed that females became bolder while males decreased their boldness as the active season progressed. These results suggest that boldness does not contribute to the habitat settlement patterns of the ornate tree lizard, but that individual boldness may fluctuate with the ornate tree lizards' seasonal activities.

My results for habitat quality are concurrent with those of a previous study by Paterson and Blouin-Demers (2018), who quantified habitat quality for three years at eight of the ten sites used in this study by measuring food availability and thermal quality. Lymburner (unpublished data 2019) found during my study that the wash habitat had a higher proportion of days in the T_{set} of the ornate tree lizard, indicative of higher thermal quality. A lizard living in the wash habitat would therefore have more opportunities to thermoregulate which is important for maintaining an optimal body temperature for all processes (i.e. locomotion, foraging, mating etc.). Although I only analysed thermal quality to determine habitat quality, this environmental characteristic has been shown to be very important in dictating habitat selection patterns (Blouin-Demers and

24   Weatherhead 2001). Spatial variations of this important abiotic factor have shown to influence

25   species distribution (Halliday and Blouin-Demers 2016; Thompson et *al.* 2018), wherein

26   individuals favor habitats providing more opportunities to thermoregulate. For example, Halliday

27   and Blouin-Demers's (2016) study on common gartersnakes found that snakes were much more

28   abundant in the higher thermal quality field habitat than in the forested habitat.

29   My results, inferring a homogeneous distribution of boldness across both habitats of

30   differing quality, contradicts the conclusions of a previous *in vitro* study on the territorial dynamics

31   of the ornate tree lizard (Taylor et *al.* 2016). Taylor et *al.*'s (2016) results suggests that boldness

32   may play a role in the geographic variation of the social and ecological dynamics of the ornate tree

33   lizard. However, their *in vitro* results may not reflect the natural population dynamics which were

34   observed in this study (Carter et *al.* 2012). Assays on animal personality will frequently use

35   individuals collected from the wild, but will complete testing within laboratory settings (López et

36   *al.* 2005; Wilson et *al.* 2010). Although these methods assume random sampling, variations in the

37   catchability within wild populations may consequently cause a systematic trapping bias and thus,

38   bias laboratory results (Carter et *al.* 2012). Additionally, differences in laboratory conditions

39   (Lewejohann et *al.* 2006) or prior experience with humans (Osborn and Briffa 2016) may hinder

40   the outcomes of *in vitro* behavioural tests. For example, a study by Fisher et *al.* (2016) on the

41   behaviour of wild field crickets (*Gryllus campestris*) found no correlation between boldness in situ

42   and in vitro settings. These discrepancies between *in vitro* and *in situ* results emphasises the

43   importance of studying behaviours in a natural setting. Nonetheless, laboratory studies are

44   important to study specific variables of interest and provide the setting to control for other

45   confounding factors. To my knowledge, Taylor et *al.* (2016) behavior assay is the only previous

46   study to have assessed the influence of boldness on the territorial dynamics of this species and is

47   thus, the best empirical source to compare my findings.

48   Although few in numbers, some studies have previously evaluated the influence of

49   boldness on habitat selection patterns (Bonnot et *al.* 2018; Seltmann et *al.* 2013; Taylor et *al*. 2016;

50   Wilson et *al.* 2009). However, a great majority of the literature is focused on the effects of habitat

51   conditions or structure on escape responses (Anchieta et *al.* 2015; Martin and Lopez 1995;

52   Stankowich and Coss 2006). These studies assume plasticity in boldness among individuals. In

53   contrast, this study assumes consistency in boldness among individuals, suggesting the behavior

54   is a "personality trait". This assumption is supported by multiple studies which found consistency

55   of boldness over both time and among situations (Kashon and Carlson 2017; Highcock and Carter

56   2014). Variance in boldness between individuals can results in differences in fitness (Bonnot et *al*.

57   2018), which can ultimately lead to selective pressures acting upon this behaviour. This is

58   exemplified in Bonnot et *al.*'s (2018) study on female roe deer (*Capreolus capreolus*), which found

59   that predation risk favored bolder females in the rich open habitats, leading to increased

60   reproductive success. Seltmann and *al.* (2013) found similar results in eider ducks (*Somateria*

61   *mollissima*), wherein bolder females nested in higher quality areas further from the shore and had

62   a higher viable proportion of the clutch. In contrast, my results showed no difference in boldness

63   between both habitats, suggesting that this behaviour does not contribute to territorial dynamics.

64   The absence of variance within the spatial distribution of boldness may have resulted form

65   elevated predation within the higher quality wash habitat, which may have counterbalanced the

66   fitness advantages of this behaviour. Boldness increases an individual's ability to exploit high

67   quality habitats despite the threat of predation (Bonnot et *al*. 2018). The higher resource and mate

68   acquisition stemming from bolder behaviours has been shown to increase reproductive success

69   (Bonnot et *al*. 2018) and therefore contribute to spatial distribution of individuals (Wilson et al.

70   2010). If this spatial distribution resulting from the fitness benefits of boldness was attributable to

71   the ornate tree lizard's ecological context, the high quality wash habitats should have been

72   occupied by bolder individuals, which is not supported by this study. The physical and ecological

73   characteristics of the wash differ from that of the upland, which may have influenced the cost-

74   benefit of boldness through increased predation. The open canopy and lack of refuges (i.e. trees)

75   increases the lizard's susceptibility to predation (Shepard 2007). Additionally, the higher thermal

76   quality of the wash habitat favors other ectotherms, including predators such as snakes. As a result,

77   the elevated predation in the wash habitat may have factored into the homogenisation of the

78   distribution of boldness across both habitats. However, this hypothesis contradicts previous studies

79   such as Harris and *al*. (2010), which observed that fish in habitats of high predation emerged sooner

80   from their shelter, thus expressing bolder traits.

81   Although no differences in boldness was observed between the two distinct habitats, bold

82   behaviours may have a more influential role at a finer spatial scale. Habitat selection occurs at

83   multiple orders including selection of home range, habitat type and feeding ground (Johnson,

84   1980). It is thus possible that boldness does not dictate the territorial dynamics of the ornate tree

85   lizard at the larger, habitat selection scale assayed in this study, but rather at a finer microhabitat

86   selection scale. Lattanzio and Miles (2014) evaluated the spatial distribution of the ornate tree

87   lizard as a function of aggression and found no significant differences in spatial network structure

88   between a lower quality unburned site and a higher quality infrequently burned site. However,

89   their finer scale analysis revealed a divergence in microhabitat use and diet, wherein aggressive

90   males usurped the higher quality trees and consumed higher trophic level prey. This variation in

91   the spatial distribution of boldness as a function of spatial scales may provide an explanation for

92   the differences in the results from my study, versus those of Taylor et *al*. (2016).

93   The results from my final model suggests that females increased, while males decreased in

94   boldness as the active season progressed. However, these observations may have been a result of

95   reproductive trade offs rather than a behavioural shift. The increase in boldness in females may

96   indicate a change in physiological conditions. During the reproduction period, female lizards will

97   invest significant amounts of energy and resources to optimize their reproductive success

98   (Landwer 1994). This investment negatively affects their physical condition which can result in a

99   reduction the efficiency of their escape response (Sinervo et *al.* 1991, Veasey et *al.* 2001). As a

100   result, females can be more vulnerable to predation during the reproductive season. A study by

101   Landwer (1994) who experimentally reduced egg production in certain female ornate tree lizards

102   found that they had higher growth rates and were significantly less likely to become prey than

103   controls. Thus, the reduction in time to capture females as the active season progressed may have

104   been due to their reduced escape efficiency rather than a change in boldness.

105   Similarly, the increase in time to capture male ornate tree lizards may not be indicative of

106   a behavioural shift but rather a result of increased predation of bolder males. Male ornate tree

107   lizards exhibit a colour polymorphism (Figure 4) associated to reproductive success (Lattanzio et

108   *al.* 2014). "Push up" displays are used by male lizards in competitive territorial interactions with

109   other males (McElroy et *al.* 2007). Competitive and mating behaviors which increase the

110   conspicuousness of males has shown to increase the risk of predation (Hedrick 2000). An increase

111   in conspicuousness coupled with high boldness may have resulted in an increase in mortality of

112   bold, male lizards. Therefore, it is possible that as the active season progressed, boldness did not

113   decrease among individuals, but rather, bold individuals were preyed upon more and suffered a

114   higher mortality (Hulthén et *al* 2017).

115   **Limitations**

116   The greatest limitation of this study is the lack of control for gene flow and migration

117   between the two habitats. In order to test the hypothesis, I used two adjacent habitats which varied

118   in quality. However, as there are no physical boundaries separating the two, it is possible that

119   movements of individuals between the upland and the wash reduced my ability to detect a

120   difference in boldness. Overall, 21% of lizards that were captured more than once were found to

121   switch between habitat types at least once. This is consistent with Paterson and Blouin-Demers

122   (2017) who, using mark-recapture methods for population density measurements of the same study

123   system, found that that 25% of recaptured individuals had on at least one occasion switched

124   habitats. Thus, the homogeneous distribution of boldness detected in my study may have been

125   caused by the flux of individuals between habitats.

126   Furthermore, although field studies can provide a more accurate depiction of ecological

127   and social dynamics (Carter et *al* 2012), it is difficult to extract a specific variable of interest while

128   controlling for all other confounding factors. This trade-off is one of the limitations of my study.

129   For example, I was unable to control for previous encounters of predation, which could have

130   affected individual boldness (Hellström and Magnahagen 2011). Thus, lizard having recently

131   experience a predation event may have expressed shyer behaviours despite their bolder personality.

132   Another limitation of my study is the method used to quantify boldness. I used a novel

133   approach of calculating the time it took to capture lizards with a rod and noose. Although time to

134   capture should be an appropriate proxy for boldness (as explained in the methods), it is possible

135   that this method did not accurately capture the differences between individuals in their boldness.

136   However, similar approaches using time to quantify boldness have been used (Carter et *al*. 2012;

137   Chapman et *al*. 2010; Klefoth et *al*. 2012; Walsh et *al*. 2018). For example, Carter et *al*. (2012)

138   quantified the boldness of Namibian rock agama (*Agama planiceps*) by calculating the time it took

139   for lizards to enter the trap. Bold individuals entered the trap sooner than shy individuals. Similarly,

140   Klefoth et *al*. (2012) quantified the boldness of common carp (*Cyprinus carpio*) by measuring the

141   time until the first bite and capture of the day. Thus, although my method is novel, variances of

142   calculating the time to capture as a proxy for boldness have previously been used.

143   **Future work**

144   Based on the results of this study, possible avenues for future work include investigating

145   boldness across an environment with a gradient of quality, possibly through an altitudinal gradient,

146   which would provide more than two populations and the separation of these populations to

147   eliminate gene flow. Using sites along an altitudinal gradient would provide varying habitats of

148   thermal quality. Also, in the laboratory or semi-natural settings it would be easier to manipulate

149   habitat quality while eliminating other potential variables to allow for assessment of lizard

150   boldness between habitat types.

151   # General Conclusion

152   In conclusion, my results suggest that boldness does not contribute to the territorial

153   dynamics of the ornate tree lizard at a habitat selection scale. The change in time it took to capture

154   male and female lizards as the active season progressed may have been an indicator of reproductive

155   trade-offs rather than a shift in behaviour. Although my field study could not control for all

156   confounding variables, to the best of my knowledge, this is the first study that has assessed the

157   influence of boldness on the territorial dynamics of the ornate tree lizard in a natural setting.

158

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Table 2. Coordinates (UTM, Zone 12R) of ten study sites in the Chiricahua Mountains, Arizona, USA where ornate tree lizards (*Urosaurus ornatus*) were studied from 1 May to 21 July 2018. Note: Map of study sites in Figure 1.

Study Site	E	N
1	667700	3530564
2	667397	3533052
3	668088	3528306
4	668081	3533752
5	673919	3530657
6	669406	3529429
7	667943	3530998
8	666727	3532199
9	668271	3530541
10	667781	3533355