

An experimental test of the ideal despotic distribution

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Summary

1. Ideal despotic distribution theory predicts that the quality of habitat controlled by territorial animals should vary depending on their competitive ability and the availability of resources.
2. In environments where resources have a patchy distribution, males that monopolize high quality territories may require less territory area than males in low quality areas. This has been a difficult premise to test in the wild owing to logistical constraints regarding manipulation of relevant resources and accurate measures of territory distributions.
3. We present results from an experimental test of ideal despotic distribution theory in a wild population of side-blotched lizards, *Uta stansburiana* (Baird and Girard).
4. We manipulated thermal resources on territories by shuttling rocks between dyads of neighbouring male territories. Manipulations created high quality territories by significantly increasing the variance in temperatures available for thermoregulation.
5. Experimentally improved quality territories (rock addition) became smaller after treatment, while reduced quality territories (rock removal) became larger.
6. Males on improved and reduced quality territories had equal numbers of females, resulting in higher densities of females on the smaller high quality territories.
7. Densities of the snake *Masticophis flagellum*, the dominant predator of *Uta stansburiana*, were higher on reduced quality territories.
8. Progeny released to experimental plots had significantly higher growth-rates and survival on experimentally improved sites relative to their neighbours on low quality territories.
9. Our results demonstrate both the ecological factors that drive the ideal despotic distribution, and the fitness consequences of high and low quality territories to lizards.

Key-words: economic defendability, ideal despot, ideal free, territory quality, territory size, thermal ecology.

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Introduction

One of the classic theoretical predictions concerning resource acquisition is that animals should occupy territories in proportion to the resources available in different habitats. This idea grew out of Orians' (1969) description of the polygyny threshold and was formally termed the 'ideal free distribution' by Fretwell & Lucas (1970) and Fretwell (1972). The ideal free distribution (IFD) assumes that there are no competitive

asymmetries among individuals and that all individuals are equally 'free' to occupy any space in the habitat. Thus, in environments where resources have a patchy distribution, relatively high quality areas are expected to contain more individuals than relatively low quality areas such that all individuals gain equal access to resources.

Although most wild populations do not conform to the assumptions of the ideal free model (Inman 1990), ideal free theory has been very useful for predicting patterns of foraging behaviour. For example, Milinski (1979) demonstrated that by adding a food source at different rates on two sides of an aquarium, he could generate an ideal free distribution among sticklebacks (*Gasterosteus aculeatus*). In cases of competitive differences among contestants, territory distributions become ideal despotic, with dominant individuals securing the highest quality territories while forcing

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less able competitors into unfavourable habitats (Fretwell 1972). This asymmetry in resource distribution occurs because individuals are no longer 'free' to occupy all parts of the habitat.

A complementary approach to studies of ideal despotism is the concept of economic defendability (Brown 1964), which suggests that an upper bound to a despot's territory size may be constrained by energetic costs associated with defending a high quality area (Fretwell 1972). The idea that territory defence may be costly is well accepted and has been tested elegantly, most notably in studies with nectar feeding birds (Gill & Wolf 1975; Carpenter & MacMillen 1976; Gill & Wolf 1977). The studies of territory energetics cited above are important, but deal only in a single currency: energy gain. The ecology of territoriality is made up of not only energy budgets, but also fitness (e.g. progeny growth and survival), depredation risk and competition among residents for access to preferred sites (Stamps 1994). The economics of territoriality should be calculated similarly in terms of fitness costs and benefits.

Experimental attempts to understand interactions between territory quality and fitness gains are rare. In particular, few studies have investigated the fitness consequences of the ideal despotic distribution (but see Andren 1990; Lin & Batzli 2001). The goal of our study was to test the following two predictions of the ideal despotic distribution: (1) increasing the quality of lizard territories should result in a decrease in territory size owing to increased concentration of resources and the energetic benefits of defending a relatively smaller area (Carpenter & MacMillen 1976; Gill & Wolf 1977). In contrast, decreasing territory quality should result in an increase in territory area reflecting the need to gain additional resources. (2) Males on experimentally improved territories should have higher fitness than males on reduced quality territories. We predicted that fitness benefits would be measurable in terms of increased survival, increased access to females and/or growth and survival of progeny on high quality territories.

We used a series of novel territory quality manipulations (Calsbeek *et al.* 2002) in a population of side-blotched lizards, *Uta stansburiana*. Rock habitat provides a valuable resource to both male and female lizards since growth rate and adult body size depend on an individual's ability to behaviourally thermoregulate (Sinervo & Adolph 1989; Sinervo & Adolph 1994). Even in areas where food is abundant, if thermal resources are limiting, metabolism and hence growth are constrained by the environment (Sinervo & Adolph 1989). A high quality territory in this population is characterized by both hot and cool spots, since animals that behaviourally thermoregulate must shuttle between various temperature regimes in order to maintain their preferred body temperature (Huey 1982; Hertz, Huey & Garland 1988; Adolph 1990). In addition, high quality territories (hereafter referring to richness of

thermal resources) should provide retreat sites from predators and ideal nest sites for females to lay their eggs. Lastly, rates of philopatry for these lizards (Doughty & Sinervo 1994) are as high as 80%, thus high quality territories should also maximize growth rates and survival of juvenile lizards. Territory quality is easily manipulated by redistributing rock habitat among male lizard territories. Our manipulations allow us to make inferences regarding the economics of territory defence in side-blotched lizards in terms of fitness gains rather than energy.

Our experimental approach to understanding territoriality was facilitated by a comparative analysis of three male throat-colour morphs present in our study population. Male side-blotched lizards develop one of three genetically determined (Zamudio & Sinervo 2000) throat colour morphs with associated territorial and mating behaviours (Sinervo & Lively 1996). Ultradominant orange-throated males are highly polygynous and control large, high quality territories. Smaller blue males tend to be monogamous mate-guarders with slightly smaller territories, while yellow-throated males specialize in sneaking behaviour and only rarely defend territories (Sinervo *et al.* 2000a). Alternative strategies allow us to capitalize on a discrete hierarchy in territoriality $o > b > y$.

Methods

FIELD

This study took place during the 1998–2000 reproductive seasons (March–May), on five replicate sandstone rock outcroppings adjacent to Billy Wright Road in Merced county, California, near Los Baños Grandes. The side-blotched lizard is a small phrynosomatid lizard that matures in one year and usually dies after only a single reproductive season. In addition to their alternative mating behaviours, males exhibit one of two alternative strategies for territoriality with different physiological and life-history trade-offs (Calsbeek *et al.* 2002). Blue males tend to be philopatric and remain on their natal site for life. In contrast, orange males leave their natal site in search of high quality territories. Orange males then attempt to usurp territories from resident males. Yellow-throated males only rarely defend territories, and usually float around the territories of orange males, the strategy against which their female mimicry is most effective (Zamudio & Sinervo 2000). We consider the differences in territorial behaviour between the morphs elsewhere (Calsbeek *et al.* 2002) and in this paper focus on the similarities in response to changes in territory quality.

Female side-blotched lizards tend to be more philopatric than males (Doughty & Sinervo 1994; Doughty, Burghardt, & Sinervo 1994) and set up smaller territories within or adjacent to the territories of males. Although male territories usually remain fixed over the course of a breeding season, females are able to move

more freely between territories and are known to do so particularly when resources are manipulated (Calsbeek *et al.* 2002; this study).

Early each spring we captured all animals on the outcroppings ($N = 22, 92$ and 103 in 1998, 1999, and 2000, respectively), recorded sex, snout–vent length (mm), mass (g) and throat colour for all individuals, and assigned a unique toe clip and dorsal paint mark. Paint marks were used to facilitate visual identification in the field, while toe-clips provide a form of permanent identification. We recorded territories for all animals by walking multiple daily transects over the entire study area. Locations of each individual animal sighting were recorded as a territory point using a compass bearing and distance measurement from a known landmark. Territories were mapped (minimum polygon method (Tinkle, McGregor, & Dana 1962; Sinervo & Lively 1996) from daily visual censuses by a single observer (mean = 7.7, 6.9 and 5.6 sightings per male based on $N = 381, 654,$ and 585 total sightings for males and females in 1998, 1999 and 2000, respectively). We consider areas occupied by blue- and orange-throated males to be territories and areas occupied by yellows to be home-ranges, based on a series of male–male introductions designed to measure territory defence (Calsbeek & Sinervo, submitted). We assigned single females to males when their territories were contained entirely within the territory of a male. A female whose territory was adjacent to two male territories was considered to be ‘shared’ by both males (Sinervo & Lively 1996). The incidence of multiple paternity within a clutch is very high in these lizards (Zamudio & Sinervo 2000) and we suggest that assigning females to multiple males is a realistic method for determining male access to females (Sinervo & Lively 1996; Sinervo 2001).

EXPERIMENTAL METHODS

After the first 2 weeks of territory mapping, we paired dyads of neighbouring males and removed rock habitat from the territories of half the males on each of four replicate outcrops and deposited it on the territories of the neighbouring male in each pair. In 1998 removals and additions were determined randomly (coin toss). During 1999 and 2000 we removed rock from territories of the larger of the two males and added it to the territories of their smaller neighbours. We removed approximately 30% of the available rock habitat from each larger male’s territory and used it to construct two to three rock additions per territory of the smaller male. Rock additions were comprised of 10–40 rocks each (mean = 15.7, $SD = 11.1$) and provided perch heights of about 0.5–1 m, which are similar to those available on naturally high quality territories frequented by males (personal observation). Rock piles were placed at the centre and near the perimeter of the male’s territory. In total, we moved approximately 820 kg of rock per experimental outcrop (total area

~2200 m²) each year. All rock manipulations were performed over a single day, except on one outcrop where manipulations were completed over the course of 2 days owing to the size of the outcrop.

Following all rock manipulations, we allowed the animals 4 days to equilibrate and settle on their new territories. This time frame has proved sufficient to allow all interactions between neighbours to stabilize (DeNardo & Sinervo 1994). Four days after the manipulations, we resumed territory mapping for all males and females on the outcrop. In addition, we monitored all rock outcroppings surrounding our experimental plots out to a distance of 1 km. This allowed us to record any dispersal events that may have occurred as a result of our territory manipulations. None were recorded.

CARE OF GRAVID FEMALES AND EGGS

Near the end of each reproductive season, we recaptured near-term gravid females. Females were housed individually in the laboratory in plastic terraria with a damp mixture of sand and peat moss, and were provided food (*Achaeta* crickets) and water *ad libitum*. Terraria were kept in an environmental chamber with a 12L : 12D photoperiod, and were provided with full spectrum fluorescent lamps and a 40-watt bulb as a heat source.

Terraria were checked daily for eggs. Eggs were placed in individual 100 mL plastic cups filled with a 9 : 1 mixture of vermiculite and water which maintains the hydric conditions (–200 kPa) that are near optimal for development (Sinervo *et al.* 1992). This mixture was changed weekly. Cups were placed in plastic boxes, wrapped in plastic bags and incubated at 28 °C until hatching (*c.* 45 days).

Upon hatching, all lizards were assigned a unique toe clip, which permanently identifies individuals. Hatchlings were weighed (g), measured (snout–vent length [mm]), sexed and released onto field plots (Table 3). Progeny were released in pairs randomly to either improved (rock added) or reduced (rock removed) quality territory treatments that had been constructed for use in that year’s study on adults.

GROWTH AND SURVIVAL

We measured mass-specific growth rates of progeny (In mass_t–ln mass₀/Δt) (Sinervo & Adolph 1989; Sinervo 1990b) from hatching date until the first recapture in spring (late February–early March). Mass specific growth rate (hereafter MSGR) measures the proportional increase in size, not absolute growth rate (Sinervo 1990a). Measuring MSGR from hatching to spring encompasses the entire growth phase from the juvenile stage to the period just before onset of the breeding season (Tinkle 1967). Previous studies have shown that MSGR may be under strong influence of maternal effects (Sinervo & Adolph 1989). In particular,

egg size has an allometric effect on hatchling growth rate (Sinervo 1990a). Hatchling mass is correlated strongly with egg mass in these lizards (data from this study: $R = 0.59$, d.f. = 42; $P < 0.0001$), and we controlled for possible maternal effects of egg size in all of our analyses of MSGR, by including \ln (hatchling mass) as a covariate in our analyses of variance.

THERMAL PROPERTIES

We constructed thermal maps of male home-ranges using lizard models with a copper-constantan thermocouple (Bailey model BAT-12) designed to measure the body temperature of a lizard. This method has been shown to be effective in numerous studies (reviewed in Shine & Kearney 2001). Models were constructed from 7.0 cm lengths of polyvinylchloride tubing (1.5 cm diameter), painted grey to mimic the heat absorbency of *Uta*, and were sealed at both ends with cork stoppers (Adolph 1990). Thermocouples were calibrated in the laboratory against a standard mercury thermometer. Thermocouple lizard models were used to sample a range of substrates utilized by lizards, including top surfaces of rock piles, cracks and retreat sites in rocks, and terrestrial habitat near rock piles. We began recording lizard model temperatures immediately following the first lizard sighting on the outcrop. Temperature measurements were then made at approximately 2-min intervals until the first model reached a temperature of 35 °C, the preferred body temperature of *Uta* (Tinkle 1967). Lizard model temperatures were then recorded every hour until the end of the day (c. 18 : 00). In total, we recorded approximately 150–200 lizard model temperature per day. We calculated the mean daily temperature of models at each substrate on experimentally manipulated territories. We also calculated the variance in model temperatures at each location as a measure of the diversity of microclimates available to resident lizards.

We monitored the presence of a predatory snake, the California coachwhip *Masticophis flagellum*, on male and female territories by recording all snake sightings as a compass bearing and distance measurement from a known landmark. Although it is extremely rare to see lizards die in predatory events, the densities of lizards decline each year soon after the first snake sightings on our outcrop. Thus, we can conclude with reasonable certainty that the coachwhip is the dominant predator on *Uta*, and is a major source of mortality in this population (see also discussion in Sinervo & DeNardo 1996; Sinervo, Svensson & Comendant 2000b). The coachwhip is a diurnal visual predator that stalks its prey by periscoping its head out of fissures in rocks. The snake's foraging behaviour made it conspicuous to an observer, and so visual censuses of snakes are a good estimate of snake activity on both high and low quality lizard territories. A total of 60 days of observation were carried out across all of the study sites for snake predators.

STATISTICAL METHODS

When behaviour is not independent of other interacting individuals, as in the case of territoriality, traditional estimates of an ecological effect arising from competitive interactions are inappropriate (Sinervo 2001). We have developed experimental and statistical protocols (Sinervo *et al.* 2000b; Svensson & Sinervo 2000) for analysing social interactions when behaviour is dependent on interactions among individual males (Sinervo & Basolo 1996). We avoid the problem of pseudoreplication (Hurlbert 1984) by estimating changes in territory size on replicate plots between dyads of males where social and biotic agents of selection are manipulated. Behavioural non-independence clearly arises when changes in the distribution of rock habitat increase intrasexual conflict arising from competition between neighbours (Calsbeek *et al.* 2002). Rather than using individual males as independent data points, our statistical reference relied on dyadic interactions between males. We compared a total of 27 dyads (i.e. 54 males) on our experimental plots and 11 dyads (22 males) on our control plot. Males whose nearest neighbour was greater than 10 m away (the diameter of a typical male territory) were not included in dyadic comparisons. Data closely approximated normality (Shapiro–Wilks test) and we use parametric statistical tests in all of our analyses. We compared changes in territory area between dyads of males using analyses of variance. We used analyses of covariance to measure differences in mass specific growth rate and controlled for the effects of egg-size and hatchling mass. Differences in survival between improved and reduced quality territories were compared with paired *t*-tests.

CONTROL

Because we mapped territories for males and females before and after rock manipulations (e.g. repeated measures design), our experiment is controlled internally for the effects of rock manipulation. For completeness, however, we mapped territories on a fifth rock outcropping on which rocks had been manipulated during the previous year. Although we could have relied on natural variation in territory quality present on the outcrops, using an experimental plot from the previous year provided us with predetermined pairs of high and low quality territories for use as a control. We prepared our control outcrop during the spring of 1999 by moving rock habitat on one of our replicate plots and allowing individuals to naturally recruit to experimentally improved and reduced quality territories. By the spring of 2000, males and females naturally occupied high and low quality spots as determined by the previous year's manipulations. Rather than moving rocks between territories, we controlled for the effects of moving rocks *per se* by randomizing the positions of existing rocks within the territories of males. Thus

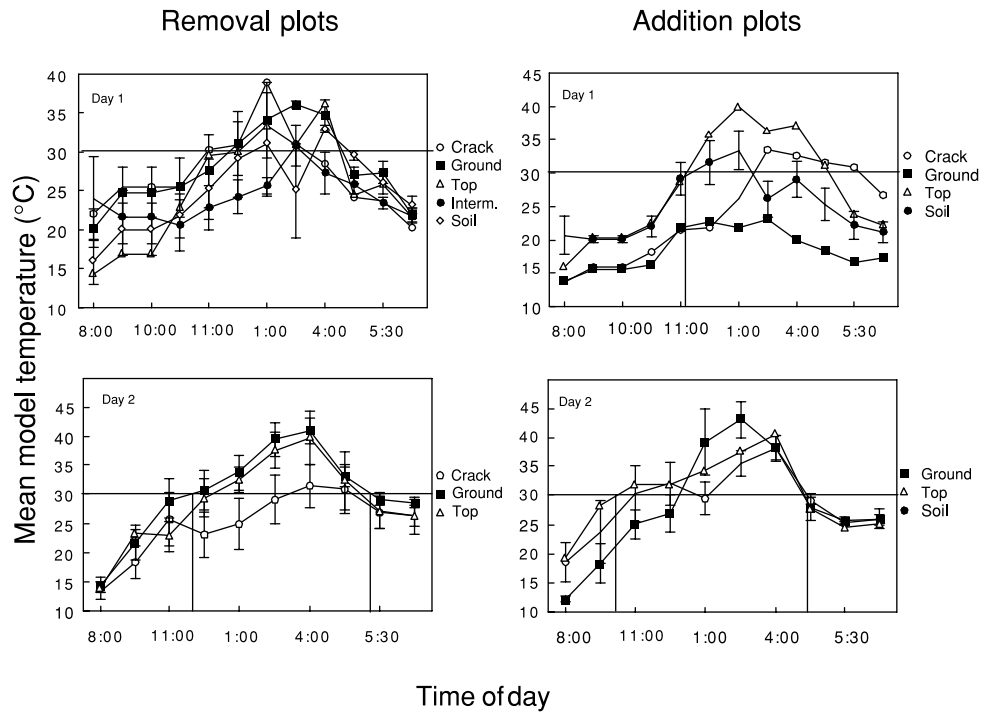


Fig. 1. Temperature profiles for two consecutive days (March 14–15) on lizard territories (showing mean temperature + 1 SE). Left panels show temperature profiles for territories from which we experimentally removed rock habitat. Right panels show temperature profiles for territories to which we experimentally added rock habitat. Mean temperatures between removal and addition plots were not significantly different ($P = 0.65$). Vertical and horizontal lines at 30 °C indicate time of day when lizards become active.

males on control plots experienced the same disruptive effects of rock movements but maintained the same territory quality. Owing to logistical constraints involved in moving large quantities of rock habitat each year, and due to the control outcrop's dependence on manipulations from a previous reproductive season, we performed our control manipulations on $N = 11$ dyads (i.e. comprised of 22 males), and compared results with 13 dyads (26 males) on our experimental outcrop that was manipulated the same year.

Results

Four lines of experimental evidence support our hypotheses regarding the ideal despotic nature of lizard territories. Our manipulations of territory quality provided a resident male on an experimentally improved territory potential access to all of the thermal benefits described above (Huey *et al.* 1989). Males competed vigorously over territory manipulations. The size of territories changed in response to manipulations of territory quality, however, the positions (e.g. centroids) of most male territories remained stable. Nearly all males (74/81 pooling across all years) that had previously defended good territories against rivals remained on their territories even after the quality reduction. In contrast, females altered the location of their territories after rock manipulations and demonstrated a strong preference for experimental rock piles (Calsbeek *et al.* 2002). Finally, progeny had higher growth rates

and survival on high quality sites relative to those progeny on low quality sites. We expand on these results below.

TERRITORY QUALITY

Territory manipulations alter the thermal characteristics of territories. The mean temperature on rock removal sites was not significantly different than on experimentally improved sites (mean = 26.1 °C and 26.7 °C on improved and reduced quality territories, respectively, ANOVA $F_{1,23} = 0.20$, $P = 0.65$). However, experimental rock additions increased the variance in temperature availability compared to rock removal sites ($\sigma^2_{\text{addition}} = 27.45$ vs. $\sigma^2_{\text{addition}} = 11.38$, $F_{23,20}$ -ratio = 2.41, critical value = 2.05, $P < 0.05$, Fig. 1) suggesting an increased range in microhabitat availability on rock addition sites as a result of rock manipulations. For example, hot sites (such as the ground) are extremely hot, but not variable, whereas sites such as cracks tend to be cool but highly variable, depending on the angle of the sun. Variance in temperature availability would provide males a wide range of thermal alternatives from which to achieve their preferred body temperature.

CHANGES IN TERRITORY SIZE

Experimental manipulations of territory quality provided support for our first hypothesis regarding

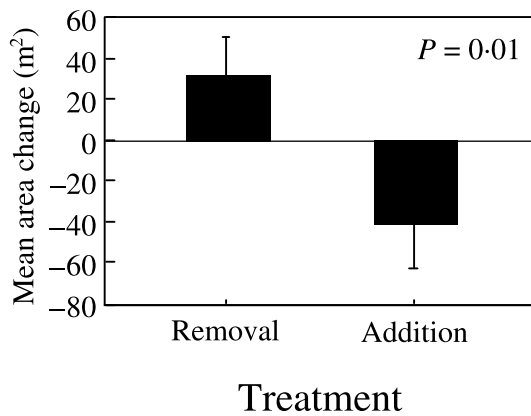


Fig. 2. Changes in territory size after rock manipulation for dyads of males on experimentally improved vs. reduced quality territories (showing treatment mean + SE). Experimental addition of rock habitat to male territories resulted in reduced territory area, while removing rock habitat had the opposite effect. This pattern of change in territory size was the same on all four replicate plots, though the difference was not significant in all years. The consensus combined *P*-value for data from all years was significant (*P* = 0.02).

changes in territory size. Because our experimental design relied on dyads of males as experimental units, we measured changes in territory size between pairs of males. Within dyads of males, adding thermal resources to one male's territory resulted in an overall decrease in territory size, while removing thermal resources from his male neighbour's territory had the opposite effect (mean area size prior to manipulation = 54 m² ± 8.36 and 76 m² ± 20.69; mean area size following manipulation = 91.6 m² ± 24.49 and 42.7 m² ± 11.6 for males on territories that were reduced and improved in quality, respectively; ANOVA $F_{1,23} = 6.17$, *P* = 0.02, plot effect $F_{1,3} = 1.48$, *P* = 0.25; Fig. 2). Differences in territory area were not an artefact of differences in visibility between treatment groups. We were just as likely to see males on improved and reduced quality territories following rock manipulations (ANOVA $F_{1,66} = 0.84$, *P* = 0.36 with all males including those not used in dyadic analyses above). We measured the same pattern of changes in territory size on four replicate plots in all three years of our study. Results were not significant in all individual years, although the patterns of change were the same. Therefore, we performed a consensus combined *P*-value test which was significant for the four experimental replicates (Sokal & Rohlf 1995) (*P* = 0.02).

On our control outcrop, male territory size did not change significantly (repeated measures ANOVA, TR × repeat $F_{1,11} = 0.60$ *P* = 0.47). However, there was a significant difference in how males on high and low quality experimental plots changed their territory area compared to males that recruited to high and low quality territories on control plots. The pattern of territory size change on our control plot was opposite to and significantly different from that of our four experimental treatments. Males that recruited to

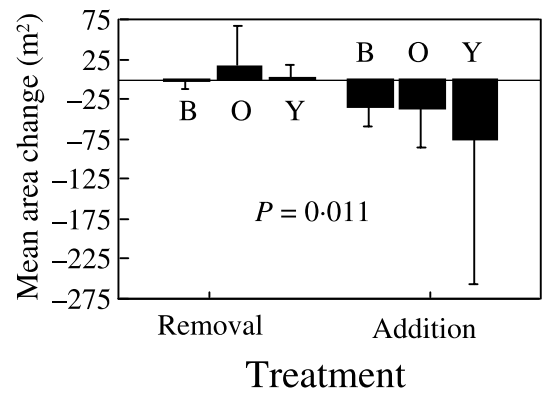


Fig. 3. Differences among the three alternative reproductive strategies in response to our experimental manipulations of territory quality (showing treatment mean for each alternative male strategy + SE). Orange males on reduced quality territories were significantly more likely than blue- and yellow-throated males to expand their territory borders in response to rock manipulations. Although all three male morphs reduced the size of their territories when rock habitat was experimentally added to territories, the response was particularly strong for yellow males. Yellow males do not specialize in territory defence (Sinervo & Lively 1996), and their response to rock manipulations demonstrates their propensity to cluster around the territories of orange males and wait for an opportunity to steal copulations.

high quality territories (i.e. those containing a rock manipulation from the previous year's experiment, see Methods) increased the size of their territories after we repositioned existing rocks within their territory boundaries (control). In contrast, males that received rocks on experimental plots decreased the size of their territories (experimental) in response to the rock additions. The opposite pattern was true of males on low quality territories. Our test of this difference (repeated measures ANOVA of TR × plot, $F_{1,23} = 4.82$, *P* = 0.04) coupled with the repeated-measures design using male dyads as experimental units provides a robust control for our experiment. Our experiment was not confounded by differences in male body size (ANCOVA $F_{1,23} = 3.07$, *P* > 0.09 controlling for the effects of mass), nor did we expect such a confound, since we measured changes in territory size rather than absolute differences of individual males.

When we consider the effects of rock manipulation on each of the three male morphs independently, the morphs respond similarly to changes in territory quality (TR × morph ANCOVA $F_{1,3} = 1.23$, *P* = 0.23; Fig. 3). However, it is apparent that orange males are the most likely to increase the size of their territories after quality reduction, while blues and yellows have a less pronounced reaction. All three male types, particularly yellow males, reduce their territory size when on territories containing an experimental rock addition (ANCOVA for Treatment, $F_{1,37} = 5.08$, *P* = 0.01). Because some individuals could not be scored accurately for throat colour, total numbers of males used in this test differ from those above.

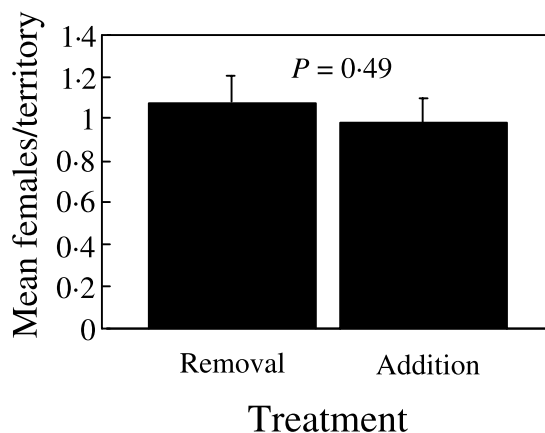


Fig. 4. Mean numbers of females on experimentally improved and reduced quality territories after territory quality manipulations (showing treatment mean + SE). Average numbers of females did not differ between improved and reduced quality territories following our experimental manipulations of territory quality. Thus, males on smaller high quality territories had higher densities of females on their territories than did males on larger low quality territories. We suggest that as most males have a single female on their territory, irrespective of territory area, that the perceived reproductive pay-offs among males are equal.

ACCESS TO FEMALES

Our second hypothesis regarding the fitness benefits of high quality territories was also supported. Females preferred rock additions and 37 of 51 females moved onto territories to which rock was added (Calsbeek *et al.* 2002). Although the net change in access to females did not differ for males on improved vs. reduced quality territories (ANOVA $F_{1,65} = 0.48$, $P = 0.49$, Fig. 4), the fact that territory size decreased after rock additions resulted in higher densities of females for males on improved territories (mean density (females/m²) = 0.04 ± 0.19 and 0.62 ± 0.22 for reduced and improved quality territories, respectively; ANOVA $F_{1,54} = 4.02$, $P = 0.05$). We also detected a significant effect of experimental plot due to the fact that females were more concentrated on some plots than others (ANOVA $F_{1,3} = 2.83$, $P = 0.04$).

PREDATION AND SURVIVAL OF ADULTS

Snake abundance was significantly higher on experimentally reduced quality territories. In total, we observed 11 individual snakes on our experimental plots, nine of which were on experimentally reduced quality territories while two were on improved territories ($P = 0.04$, Table 1). Nevertheless, males on reduced quality territories were significantly more likely to survive until females became receptive (about one week post-manipulation) than were males on experimentally improved territories ($P = 0.047$, Table 2).

PROGENY GROWTH AND SURVIVAL

Our hypothesis regarding the fitness consequences of territory quality was supported further by differences

Table 1. G-table summary of unique observations of the primary predator on *Uta stansburiana*, the coachwhip snake, *Mastacophis flagellum*. Snakes were significantly more likely to appear on our experimentally reduced quality sites than on experimentally improved sites. We recorded snake sightings during 60 total days of territory observations, making equal numbers of visits to both improved and reduced quality territories

Experimental treatment	Snakes observed	Observation days
High quality territories	9	60
Low quality territories	2	60

$G^2 = 4.44$, $P = 0.04$.

Table 2. Contingency χ^2 summary table of male survival on experimentally improved and reduced quality territories. Males on experimentally improved territories were significantly more likely to die during the week following our territory manipulations

Experimental treatment	Number of males	
	Alive	Dead
Low quality territories	31	15
High quality territories	19	22

$\chi^2 = 3.92$, $P = 0.047$.

in growth and survival among progeny. There were no differences in size among hatchlings when they were released initially to improved vs. reduced quality territories (e.g. from 1998 ANOVA $F_{1,32} = 0.44$, $P = 0.55$), reflecting the fact that we randomized all hatchlings prior to release. During 1999 we recaptured 25 of the 42 progeny (60%) that we released in 1998. From the period of hatching to the first recapture in spring, juvenile MSGR was significantly higher on experimentally improved home-ranges than on reduced quality home-ranges (ANCOVA $F_{1,22} = 6.26$ $P < 0.02$; covariate for hatchling mass $P < 0.001$). The next year California experienced a severe drought, and rainfall, which normally begins in September, did not begin until mid-December. Consequently, lizard densities were extremely low on all rock outcrops. During spring of 2000 we recaptured nine of 67 lizards (13%) that had been released in 1999. However, even with this small sample size, differences in MSGR between reduced and improved quality home-ranges were significant (ANOVA $F_{1,7} = 5.99$ $P < 0.05$). Finally, during the spring of 2001, we recaptured 25 of the 73 hatchlings (34%) that had been released in 2000. Again, juvenile MSGR was significantly higher on experimentally improved home-ranges than on reduced quality home-ranges (ANCOVA $F_{1,22} = 4.38$ $P < 0.04$; covariate for hatchling mass, $P < 0.02$). The consensus combined P -value for all three years was significant ($P < 0.005$; Fig. 5).

During 1998 and 1999 overall body size (mass) of progeny was also significantly different between treatments.

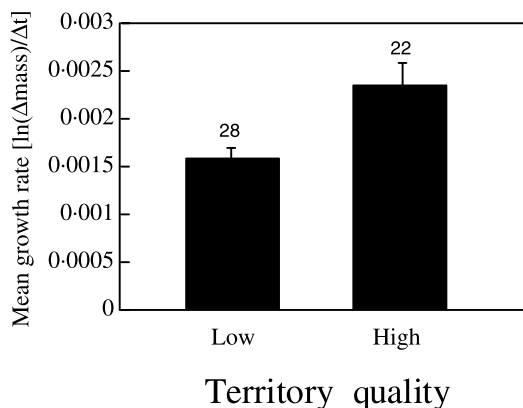


Fig. 5. Differences in mass specific growth rate on experimentally improved and reduced quality territories in juvenile lizards. Growth rates were significantly higher for hatchlings on experimentally improved territories compared to hatchlings on reduced quality territories (controlling for maternal effects due to hatchling mass). Error bars indicate one standard error. Numbers above error bars indicate the numbers of progeny captured from each treatment.

Data for 1998 ($X_{\text{improved}} = 6.58 \text{ g} \pm 0.37$ vs. $X_{\text{reduced}} = 5.54 \text{ g} \pm 0.40$, ANOVA $F_{1,22} = 6.42$, $P < 0.02$; covariate for hatchling mass $P < 0.001$). Data for 1999 ($X_{\text{improved}} = 5.15 \text{ g} \pm 0.25$ vs. $X_{\text{reduced}} = 2.76 \text{ g} \pm 0.47$, ANOVA $F_{1,7} = 6.64$ $P < 0.05$; covariate for hatchling mass $P < 0.001$). Body size of progeny did not differ between treatments during 2000 ($P = 0.2$).

Finally, progeny survival differed between improved and reduced quality home-ranges. We recorded survival during the fall of 2000. Hatchlings released to high quality home-ranges were significantly more likely to survive to our fall census than hatchlings that were released to neighbouring low quality home-ranges (paired *t*-test on the proportion of surviving individuals from adjacent high and low quality plots, $t = 3.01$, d.f. = 7 $P < 0.02$, Table 3).

Discussion

After four decades of study, understanding the role of ecology in predicting the distribution of animal

territories remains a central problem in biology (Koops & Abrahams 1999). Ideal despotic distribution theory predicts that competition for territories should result in dominant residents occupying high quality areas while forcing weaker competitors into less favourable habitats (Fretwell 1972). A cost–benefit approach to territoriality provides the conceptual basis for gauging the quality and defendability of a territory (Schoener 1983). We have therefore taken a two-pronged approach in our analyses of territory distributions, considering both the ecological factors contributing to the evolution of territorial behaviours, and the fitness consequences of territory quality to lizards.

Males that received experimentally improved territories reduced the overall size of their territories after our manipulations. In contrast, males whose territory quality was reduced owing to experimental loss of rock habitat expanded their territory boundaries (Fig. 2). This result suggests that male territory size may be influenced in part by the amount of high quality thermal resources available on territories. Indeed, we measured significant differences in the thermal characteristics of our experimentally manipulated territories (Fig. 1). Patterns of lizard thermoregulation are dynamic, and temperature preferences may vary over extremely fine scales (Adolph 1990). Thus, increasing the range of available microclimates available to lizards on rock addition sites could allow residents to maintain their preferred body temperature more easily than on lower quality sites (Waldschmidt & Tracy 1983).

Although territory quality is likely to be affected by several additional factors (e.g. exposure to wind, food availability), we have shown that rock habitat is an excellent resource to use in manipulations of territory quality. Males on high quality territories may also be able to defend resources at a lower physiological cost relative to males on larger, low quality territories (Brown 1964). Previous work on golden-winged sunbirds (Gill & Wolf 1975) and Hawaiian honeycreepers (Carpenter & MacMillen 1976) has also demonstrated that an upper limit to territory size may be determined by costs of defending a large area. Although our results are compelling, they do not rule out alternative

Table 3. Numbers of juveniles released and recaptured at each high and low quality treatment between dyads of home ranges. The proportion of individuals that survived on high vs. low quality plots reflects the difference in probability of survival due to home range quality and was compared using a paired *t*-test

Dyad	Hatchlings released		Numbers survived		Proportion survived	
	Good sites	Poor sites	Good sites	Poor sites	Good sites	Poor sites
A	9	4	8	3	0.889	0.750
B	4	5	3	1	0.750	0.200
C	4	4	3	2	0.750	0.500
D	6	4	3	3	0.500	0.750
E	4	4	2	0	0.500	0.000
F	4	2	3	0	0.750	0.000
G	2	2	2	1	1.000	0.500
H	13	3	7	1	0.538	0.333

explanations for changes in space use. In the future, hypotheses regarding the energetics of territory defence could be tested using doubly labelled water (Nagy 1983) to complement our studies of fitness costs and benefits.

Males on reduced quality territories had a significantly higher probability of survival to the first clutch following territory manipulations than males whose territories were experimentally improved. This difference was only marginally significant and should be interpreted cautiously. However, it does raise an interesting question regarding the realized fitness of males on high and low quality territories. Males that survive to the first clutch may gain a fitness advantage over their rivals since mate guarding reduces the likelihood of cuckoldry by neighbouring males (Sinervo & Lively 1996). Males that died prior to the first clutch had no such guarantees. The high rates of mortality in this study are not the result of our experimental manipulations *per se*. Mortality is very high each year at the end of the breeding season, and by the following spring nearly all adults from the previous year are dead (Sinervo *et al.* 2000a).

We suggest tentatively that differences in survival may be due to increased predation by snakes on improved territories. Although observing predatory events is an extremely rare occurrence in the wild, we consistently measure a reduction in lizard densities each year following the first snake sightings on the study site (Sinervo *et al.* 2000b). Moreover, presence of snakes is known to increase mortality of gravid females owing to the reduction in escape efficiency imposed by egg load (Miles, Sinervo & Frankino 2000). Fox (1978) showed that side-blotched lizards that limited their total activity time during the day experienced higher survival relative to more active males. Waldschmidt & Tracy (1983) suggest that this difference in activity may result in reduced predation on less active males. In our study population, orange-throated males are more active than the other two morphs, and have lower between-year survival (Sinervo & Lively 1996; Sinervo *et al.* 2000a). An alternative interpretation of our survival results is that our territory manipulations led to male dispersal off the outcrop. However, we monitored all suitable lizard habitat out to 1 km from our experimental outcrops and did not capture any males from this study.

In contrast to the observed differences in adult survival, progeny on experimentally improved territories had a survival advantage relative to progeny on experimentally reduced quality territories. This difference may be due to shifts in the predator regime. By the end of summer, when hatchlings are released to the field, snake activity is greatly reduced and snake depredation is less likely to play an important role in lizard mortality. In fact, no snake has ever been observed on our study plots after early September (Sinervo, unpublished data). Fox (1978) has shown previously that juvenile lizards gain a survival advantage on home-ranges with increased structural heterogeneity. It is likely that

structural heterogeneity in the form of rock piles may also influence survival in these lizards by providing additional retreat sites from predators and extreme temperatures.

At this point it is perhaps useful to consider the role of the three alternative male strategies in the dynamics of our territory results. Considering the three male morphs independently reveals that a large proportion of the variation in territory behaviour that is unexplained by our rock manipulations arises from interactions between orange- and yellow-throated males (Fig. 3).

Orange males employ a 'usurping' strategy (Calsbeek *et al.* 2002), in which they assess territory quality over a relatively large spatial scale and usurp high quality territory resources from competitors. The increase in territory size after experimental quality reduction is greatest for orange males because their despotic strategy makes them most capable of expanding their territory boundaries in order to sequester additional thermal resources. In contrast, blue- and yellow-throated male territories change much less dramatically in size owing to an inability of these males to overcome the strong home-field advantage (Davies 1978) of their neighbours. When rock is added experimentally to territories, however, all three of the alternative morphs reduce the size of their territories. This pattern is particularly strong for yellow males for whom territory acquisition is an extremely rare occurrence (Sinervo *et al.* 2000a; Calsbeek *et al.* 2002). Yellow males do not specialize in territory defence, but using female mimicry are able to float around the territories of orange males and steal copulations through subterfuge (Zamudio & Sinervo 2000). The reduction in yellow male territory size verifies the fact that yellow males may settle in one spot once they have obtained access to females (Sinervo *et al.* 2000a).

We have presented what is, to our knowledge, one of the first experimental manipulations of territory quality with associated effects on the distribution and fitness of territorial males. Our results illustrate that two key predictions of the ideal despotic distribution are met in this population of lizards. Territory area and fitness indices both change after experimental manipulations of territory quality. We suggest that future studies of territoriality should attempt to manipulate ecologically relevant resources (e.g. habitat structure), and in addition should consider the potential fitness payoffs to territorial residents.

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