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The ontogeny of territoriality during maturation

Abstract Territoriality drives the evolution of many mating systems, yet has remained an extremely difficult trait to measure in the wild. Classic studies rely on the theoretical framework of resource holding potential (RHP) as a predictor of success in territory acquisition. However, mounting evidence suggests that an individual's RHP may change over short time scales. Previous studies suggest that RHP is best understood by considering two categories of territoriality, resource defending and resource usurping potential (RDP and RUP, respectively). In a population of the side-blotched lizard, *Uta stansburiana*, blue-throated males defend territories near their natal site (RDP) while mature orange-throated males use their RUP to sequester high quality territories from defending territorial males. We tested differences in territoriality by releasing pairs of maturing male lizards onto experimentally altered territories that had improved thermal qualities owing to the addition of rock piles. Dyads of males competed for these thermal resources and the females that were released on rock piles. Early in the season, when throat colors were not yet fully expressed, large male body size predicted contest victories irrespective of throat color. This pattern changed however, with the onset of the breeding season and maturation of throat color. Orange males tended to usurp territories from blue males within 2 weeks of contest initiation. Large male body size still influenced these contests, but after one more week, throat color was the sole factor explaining variance in territory ownership. We demonstrate the ontogeny of territoriality relating to body size and throat color during maturation, and suggest a novel approach to assessing territoriality and aggression in the wild.

Territoriality is one of the most important forces driving the evolution of mating systems. After decades of classic studies in behavioral ecology, the genetic and ecological factors that drive territorial behavior remain a central, but poorly understood realm of animal behavior (Davies and Houston 1978; Maher and Lott 1995; Stamps and Krishnan 1998). Determining the phenotypic and ecological variables that influence territorial behavior is extremely difficult, and experimental manipulations that test differences in territoriality are rare (Davies and Houston 1978; Stamps and Krishnan 1995). Most studies have relied upon correlational support and inferences regarding contest asymmetries in assessing aggression and territoriality in nature (Petrie 1984).

Maynard-Smith and Parker's (1976) game theoretic approach to territoriality, proposed three asymmetries that are important to the outcome of animal contests:

1. Asymmetry in resource value among individuals. If a contested resource is more valuable to one contender than the other, then the outcome of a contest will most likely favor the individual more willing to risk a cost in order to gain the resource.
2. Asymmetry in "resource holding potential" (RHP). Intrinsic differences in traits such as body size or fighting ability lead to a competitive asymmetry in competition over resources.
3. Uncorrelated asymmetries. Residency on high quality territories is associated with extrinsic factors such as arrival time. Early-arriving males secure the best territories on the breeding ground.

Abundant evidence exists to support the notion of RHP (Dugatkin and Biederman 1991; Ewald 1985), and many empirical studies have demonstrated the importance of body size in territorial contests (Chellappa et al. 1999;

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Reichert 1982; Stamps and Krishnan 1994a). However, most studies largely rely on correlations of an intrinsic difference (e.g. body size) between competitors and the benefits gained through residency on high quality territories (e.g. access to mates, nest sites, food). Correlational patterns are insufficient evidence for real competitive advantages over rivals, since both value asymmetries and uncorrelated asymmetries (Maynard Smith and Parker 1976) can have the same qualitative pattern as differences in RHP. Furthermore, RHP may not result from a single phenotypic character, and in some cases can be a dynamic property of an organism (e.g. expression of genetic morphs). In cases where traits that lead to RHP change over the course of a breeding season, such correlations may lead to erroneous conclusions regarding RHP.

We have shown elsewhere that RHP can be decomposed into two categories: resource defending potential (RDP) and resource usurping potential (RUP; Calsbeek et al. 2002). RDP is a defensive strategy in which territory residents defend resources against competitors. In contrast, RUP is primarily an offensive strategy in which individuals seek out high quality territories and usurp them from defending residents. The ability to usurp may be related to dominance and should result from increased fighting ability (Enquist and Leimar 1983), and/or signals such as a badge-of-status (Rohwer and Rohwer 1978). Because individuals that usurp territories from neighbors must then defend the territories against rivals, we recognize that the two strategies have common attributes. However, we distinguish them as discrete alternatives based on (1) the ability to usurp and (2) different trade-offs associated with each strategy. For example, usurping may require elevated levels of testosterone (Moore and Thompson 1990) which can be physiologically costly (Marler and Moore 1991). Thus, males that usurp territories may gain increased access to resources (i.e. territories and females), but consequently experience survival costs. In contrast, defenders require lower levels of testosterone to maintain territories. Defenders are likely to have access to fewer females and may have lower reproductive success, but because defenders do not suffer the same survival costs as usurpers, reproductive trade-offs may be less severe (Calsbeek et al. 2002). Thus, the two strategies differ in their ability to usurp, and experience different trade-offs as well.

Here we describe changes in usurping and defending behavior in side-blotched lizards, *Uta stansburiana*, over the course of a breeding season. In this system, three alternative throat color morphs of males exhibit clear differences in territorial behavior (Sinervo et al. 2000a). The morphs have a strong genetic basis that appears to arise from a single Mendelian locus (Sinervo and Zamudio 2001; Zamudio and Sinervo 2000). Two of the alternative morphs, blue- and orange-throated males, exhibit territorial strategies, while a third yellow-throated morph employs a non-territorial sneaker strategy (Sinervo and Lively 1996; Sinervo et al. 2000a).

We used novel territory quality manipulations and staged contests between male lizards to measure differences in territorial behavior among males. In our dichotomy, orange males have high RUP and adopt the USURP strategy, whereby individuals leave their current territory and sequester higher quality territories from neighbors. In contrast, blue males have high RDP and choose instead to DEFEND, a strategy by which males already on good territories protect resources from competitors. Furthermore, we predict that because yellow males do not explicitly defend territories (Sinervo et al. 2000a) they should not win in contests against orange or blue males. Consequently, the three strategies have very large asymmetries in competitive ability (Zamudio and Sinervo 2000). Competitive asymmetries arise from transitive differences between morphs in circulating levels of testosterone (orange > blue > yellow; Sinervo et al. 2000a). Endocrine differences between morphs allow us to predict a priori the territorial strategy that should be employed by different males.

The determinants of territory quality in lizards are relatively straightforward. For lizards, as for all terrestrial ectotherms, growth rate and adult body size depend on an individual's ability to thermoregulate (Adolph and Porter 1993; Sinervo and Adolph 1994). Even in areas where food is abundant, if thermal resources are limiting, metabolism and hence growth are constrained by the environment (Sinervo and Adolph 1989). High quality territories are characterized by both hot and cool spots, which allow for behavioral thermoregulation. This allows male lizards on good territories to increase total activity time, forage and court females for a greater portion of each day (Ruby 1984; Waldschmidt et al. 1986). In addition, high quality territories should provide retreat sites from predators as well as ideal nest sites for females to lay their eggs. Our manipulations of territory quality provide resident males access to all of these benefits on experimentally improved territories (Huey et al. 1989).

To measure the ontogeny of territorial behavior during maturation among the three male-strategies in this system, we initiated contests between pairs of males on high quality territories in the wild. Many studies have found that previous winners in animal contests tend to remain winners in future contests (e.g. Olsson and Shine 2000). We tested the relative ability of each male morph to take over and/or defend resources as a function of throat color and body size, by redistributing rock habitat between winners and losers after contests had equilibrated. Our experimental manipulations of territory quality allowed us to partition the episodes of male-male competition into three phases of the adult life-history: (1) prior to throat color expression, (2) immediately following the expression of throat color, and (3) immediately following the onset of the breeding season. We discuss our results in terms of the changing roles of body size and throat color expression in territoriality and consider our results in terms of ESS models of male assessment.

Materials and methods

The side-blotched lizard is a small iguanid lizard that matures in 1 year and dies after only a single reproductive season. We studied territorial behavior in side-blotched lizards during the spring of 2000, on two 300-m-long outcroppings of sandstone adjacent to Billy Wright Road in Merced County, California, near Los Baños Grandes. The outcroppings of rock that make up our study site are extremely simple ecologically. Territories are composed of little more than solid rock and loose boulders (up to 2 m in size) that are patchily distributed over grassland.

Autumn rainfall normally begins in September. However, in 1999 following a severe drought in California during which rains did not begin until mid December, lizard densities were extremely low on all rock outcrops. The following spring we captured all animals naturally present on our two experimental outcroppings ($n =18$ and 14) as well as from outcroppings in surrounding areas ($n =72$). We recorded sex, snout-vent length (mm), mass (g), and throat color for all individuals, and assigned a unique toe clip and dorsal paint mark. Paint marks were used to facilitate identification in the field, while toe-clips provided a form of permanent identification. The initial period of capturing and recording territories took place during the first 2 weeks of March. Prior to the breeding season, a few sub-adult males naturally disperse from field areas and move onto outcrops. Those males that arrived during this period were recorded as late comers and were included in the study. Males do not immigrate as adults (Doughty and Sinervo 1994).

Male throat colors begin to appear early in spring (mid March). The intensity of throat color expression increases as females become receptive to mating. All male throat colors were scored at the onset of the breeding season (and at each capture thereafter) as either blue, orange, or yellow by recording the color displayed on the underside of the male's throat and/or sides (Sinervo and Lively 1996). Male throat color is highly heritable ($h^2=0.86$; Sinervo and Zamudio 2001; Zamudio and Sinervo 2000).

To test our ideas regarding differences in territorial behavior, we staged a series of contests among males. We removed approximately 30% of the available rock habitat from a territory and used it to construct two to three rock additions on the perimeter and near the center of the neighboring territory. Each rock addition was composed of 10–40 rocks (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). We manipulated territories that had been defended by males in the year preceding our experiment thus ensuring that the distribution of manipulated territories would approximate the natural distribution of males on the outcropping. Adding rock piles to a male's territory increased the quality of that territory relative to a neighboring territory that underwent rock removal. Improved territories improve progeny growth rates and survival (Calsbeek and Sinervo 2002) and males and females both demonstrated a strong preference for our experimental rock additions. We used this preference as an index of territory quality in the current experiment. Quantitative accounts of the changes in female behavior after rock manipulations are discussed in detail elsewhere (Calsbeek et al. 2002; Calsbeek and Sinervo, submitted for publication).

There is some confusion in the territoriality literature concerning the terminology "home-range" versus "territory" when describing animal distributions (Maher and Lott 1995). "Home-range" typically describes all of the area in which an animal regularly moves, while "territory" is usually reserved for the area that an individual actively defends as exclusive space (Fox 1983; Sheldahl and Martins 2000; Stamps and Krishnan 1998). In a separate experiment, to verify that our estimates of territory distributions were not simply home-ranges, we introduced one of five different tethered male lizards onto various points inside and around the territory boundaries that we recorded (Brooks and Falls 1975). All introductions took place during the breeding season on a separate outcrop not used for experimental contests, and intruders were always strangers (Brooks and Falls 1975). Using a foreign male

Table 1 Throat scores and sample sizes of the 26 male pairs released to experimental field manipulations (*o* orange, *b* blue, *y* yellow)

Throat scores	*n* (pairs)
o versus o	2
o versus b	9
o versus y	5
b versus b	5
b versus y	4
y versus y	1

ensured that no individual had prior experience with the intruder. No intruder was used in two consecutive trials, and each resident male was tested only once. We measured the resident's response to the intruder at the center and periphery of his territory. We scored the frequencies and types of displays by both males including typical aggressive displays like extension of the gullar fold, back arching, head-bobs, push-ups, chases, and biting attempts. To prevent injury, the tethered intruding male was removed before any attack could take place. All introductions were performed on the territories of blue-throated males.

Contest one

After all animals had been captured and processed, we paired males according to body size and released the pairs of males along with two females to each of the rock addition sites that we had constructed. Male pairs (dyads) were deposited onto territories haphazardly, except that we size-matched males to within 2 mm snout-vent length (SVL), and none of the males were released within 100 m of their original site of capture. In this way, males were randomized with respect to throat color, and females were also assigned randomly to male pairs. Furthermore, none of the lizards held prior residence on their new territories. In total we released 26 pairs of males and 26 pairs of females to our experimentally manipulated territories (Table 1). Because animals were captured from neighboring outcrops, morph frequencies on our experimental plots matched morph frequencies on natural plots (57% blue, 25% orange, 18% yellow). In addition, the density of animals released (290 adults/hectare) was comparable to that naturally present on our experimental outcrops in previous years (300 adults/hectare during 1999, 220 adults/hectare during1998). Thus, treatment effects due to throat color frequency and density would not have confounded our results.

After all contests had been initiated, animals were allowed 4 days to equilibrate and settle on their new territories. This time frame has proven sufficient to allow all interactions between neighbors to stabilize (DeNardo and Sinervo 1994). We then proceeded to record territories for all animals by walking multiple daily transects over the entire study area. Territory distributions were mapped from daily visual censuses by a single observer (mean =5.6 sightings per male based on $n =585$ total sightings for males and females). Locations of each individual animal sighting were recorded as a territory point using a compass bearing and distance measurement from a known landmark. Territory distributions were computed from the minimum convex polygon (Tinkle et al. 1962) that circumscribed all of the mapped sightings for males and females. We measured territory distributions for all 104 animals in our study. Side-blotched lizards are active throughout the entire day (Fox 1978; Parker and Pianka 1975) and it is unlikely that any lizards were missed on any given day of territory data collection. Lizards that were not seen for five consecutive days were never seen thereafter, and were considered to have died. In addition, we monitored all rock outcroppings surrounding our experimental plots out to a distance of 1 km. This allowed us to record dispersal that may have occurred as a result of territory manipulations. None were recorded.

We used an unambiguous measure of contest outcome in the field experiment. Because territories are comprised of rock habitat patchily distributed over uninhabitable grassland (Sinervo et al. 2000b) only a single male can ultimately reside on an experimental

rock pile. Thus, the outcome of territory contests provided clear winners and losers (Lindstrom 1992). Winner and loser effects have been shown to be extremely important in other systems and are discussed in detail elsewhere (Hsu and Wolf 1999). A male was considered to have won a contest if he established a territory around an experimental rock addition. If a male did not control an experimental rock addition, he was considered to have lost the contest. Contest losers all continue to defend their low quality territories (Calsbeek and Sinervo, submitted for publication). A male was considered to have usurped a territory, when he appeared on a territory previously occupied by another male that had defended that territory against his rivals. In addition, former resident males whose territories were usurped had to appear elsewhere on the outcrop to rule out the possibility that a resident died, leaving a vacancy for an otherwise presumed "usurper". Evicted males often bear the scars of battle (e.g. bite marks, tail loss) suggesting that many territorial disputes escalate to costly fighting.

Competition following contest one

During the first 2 weeks of territory measurements, we recaptured all animals on the outcrop twice (on days 5 and 15). We scored throats, measured and weighed all animals to assess growth differences over these 5- and 15-day time-periods, and immediately released them to their site of capture. We also continued to monitor the outcrops for changes in residency on high and low quality territories and noted the occurrence of any usurpations of high quality territories by contest-one losers. The 2 weeks following initiation of contest one marks the approximate time each spring that males begin to express throat color (Sinervo et al. 2000a). Thus, a change in phenotypic display intensity was expected to lead to changes in territorial behavior.

Contest two

Two weeks after the start of contest one, we initiated a second round of territory contests by removing rock manipulations from territories of the contest winners, and depositing it on the neighboring territories of males that had not managed to sequester a high quality territory. The manipulation effectively reversed the outcome of the initial territory contests. This experiment specifically tested the hypothesis that the usurper strategy of orange males could overcome the loss of high quality rock, and takeover the adjacent territory of the male that received the rock. The numbers of rocks and approximate sizes of rock piles were equivalent to those used in the first contest (see above), and rocks were brushed off and rearranged to account for visual cues and scent marks that residents may have associated with rocks. All manipulations were performed in a single day, and lizards were allowed another 4-day equilibration period during which time no territory data were recorded. To control for the effects of rock manipulations, we moved rocks on a separate control outcrop but only rearranged the rocks within male territories. No changes in territory quality were made on our control outcrop.

Four days after the manipulations, we resumed territory mapping as before, again recording winners and losers based on the presence or absence of experimental rock additions within a male's territory. We also recorded territory usurpations exactly as before. At the end of the experiment, we recaptured all individuals from the outcrop for a final assessment of changes in body size. We used mass-specific growth rates [$(\ln \text{mass}_2 - \ln \text{mass}_1)/\Delta t$] to calculate changes in mass and snout vent length over the course of our study (Sinervo and Adolph 1989). After log transforming all size data, we regressed changes in mass on change in snout-vent length. We then calculated the residuals about this regression line and considered the residuals to be a measure of shape. Though use of mass × length residuals to estimate condition has come under recent criticism (Darlington and Smulders 2001; Green 2001), residuals are a size-specific measure of shape that indicate mass as a function of length, and better represent growth differences among

males. Moreover, using residuals as an estimate of condition may provide additional information regarding RHP (Maynard Smith and Parker 1976), and fighting ability in general (Marden and Rollins 1994).

Statistical methods

Contest data (win/lose) are binomial and may violate the assumptions of parametric statistics (Sokal and Rohlf 1995). We therefore used logistic regression (Hardy and Field 1998) in our analyses of contests and body-size data. We tested the prediction that territorial usurpers were most likely to be orange-throated males by randomizing the observed territory usurpation results across throat identities of males in our experimental populations. Our randomization test entailed 6 random draws without replacement from a pool of 54 throat scores. Each random draw accounted for one of the usurping events that we witnessed on our experimental plots. Throat scores in the pool were identical to throat color frequencies observed in nature. We calculated the probability that all 6 observed territory usurpations would be by orange-throated males with 1,000 randomizations.

Results

Territories versus home ranges

During 10-min trials, resident males were more likely to initiate attacks against intruding males when the intruder was placed at the center of the territory than on the perimeter. We conducted 21 trials with an intruding male on a resident male's territory. Twenty trials resulted in head-bobs, push-up displays and/or attacks initiated by the resident male towards the intruder, regardless of whether the trial took place at the center or on the perimeter of the resident male's territory. Previous introductions of tethered males in the vicinity of yellows have aroused no response from the yellow resident, while presenting a tethered intruder to orange-male residents results in a much shorter latency to attack than for those trials reported here for blues (Sinervo and Miles, unpublished data). Although data from introductions were not used to make conclusions about the nature of different territorial strategies in this study, we conclude that our estimates of territory size for males are indeed "territories" for the two territorial morphs and should not be interpreted as "home ranges". However, the areas in which yellows are found are not territories but home ranges.

Contest one outcome

Males competed vigorously over experimentally improved territories (personal observation). Male-male competition involved instances of prolonged head-bob and push-up displays that often escalated to fighting (e.g. bites). Males bear scars from bites on their head, abdomen and tail for weeks after the conclusion of these contests. Many contests were observed in the field, but contest outcomes were easily ascertained by observing which males resided on rock additions and which males
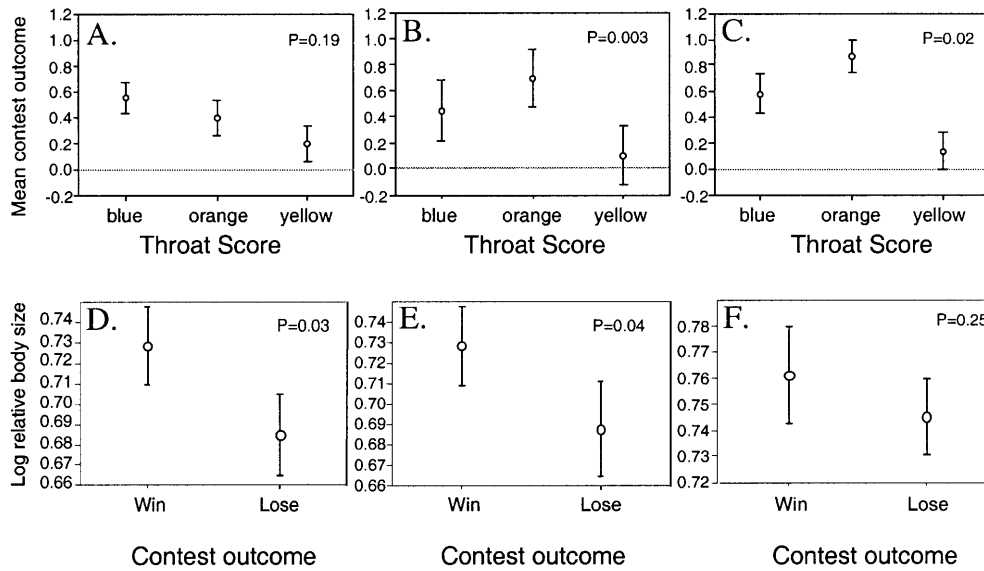
Fig. 1A–F The relative roles of male body size and throat color change over the course of the breeding season. Four days after territory contests were initiated, large male body size was a strong predictor of contest victory (**D**), while throat colors had yet to fully develop and were not important to contest outcome (**A**). A week later, as throat colors matured, body size played a less important role than earlier in the season (**E**) and the best predictor of territory ownership was orange throat color (**B**). By the end of the experiment, throat color was the sole variable that predicted territory ownership (**C**) and body size no longer differed significantly among contest winners and losers (**F**). All panels show mean values (plus or minus 1 SE) for log difference in body size (g) and contest outcome (win =1, lose =0)

occupied less favorable territory. Assessment of contest winners and losers was unambiguous since the addition and removal of rock habitat set up clear disparities in territory quality between neighboring males. After the initial 3–4 days of territory disputes, physical fights between males were observed only rarely.

Less than a week after the first contests were initiated on the outcrops, male throat colors were not yet fully expressed. At this point, male body size played the most important role in deciding contest outcome. Owing to their increased fighting ability, large males were more likely to win control over the high quality territories than were their smaller competitors (mean difference =0.53 g, logistic regression r^2=0.21, P =0.03; Fig. 1D). Male throat color had no detectable effect on winning versus losing, and all three male types were equally likely to reside on a high quality territory (G^2=2.595 P =0.27; Table 2).

Territory changes between contests

Over the course of the next week, male throat colors increased to full expression with the onset of the breeding season. At this point we observed seven territory usurpations by orange-throated males that had previously lost contests over rock additions. Orange males were ob-

Table 2 Summary of contest outcomes over two rounds of competition among orange-, blue- and yellow-throated males. After contest one, males of all three throat colors were equally likely to have won contests for territories (Fig. 1A; contingency chi-square P =0.28) while body size strongly determined contest outcome (Fig. 1D). The week following contest one revealed a strong tendency for orange males to usurp territories from blues (Fig. 1B; P <0.003). During contest two, large body size was still a strong predictor of contest victory (Fig. 1E). Contest two represents outcomes after experimental redistribution of thermal resources on territories. Orange males maintain usurped territories throughout the season. After contest two, body sizes did not differ significantly among males (Fig. 1C) and throat color was the sole predictor of territory ownership (Fig. 1F; P <0.03). Numbers of males vary over the course of the experiment due to immigration after contest one and attrition during contest two

	Contest 1		Between contests		Contest 2	
	Win	Loss	Win	Loss	Win	Loss
Orange	10	8	14	5	7	1
Blue	5	9	9	9	7	4
Yellow	3	8	1	10	1	5
	P =0.273		P =0.001		P =0.020	

served moving onto the territories of other males and displacing those males from the high quality rock habitat. The most extreme example of these incidents involved a small orange male usurping a blue male 10 days after the first contest, being joined by another small orange male the following day, both males only to be usurped by a large orange male 3 days later. This male then maintained the two territories for the duration of the breeding season. By the end of the second week of the study, orange males were significantly more likely to control high quality territories than expected by chance (G^2=12.986, P =0.001; Table 2). In addition to the role of throat color, large male body size also played a significant part in determining contest outcome. Large males were still more likely to have secured a high quality territory than were small males (mean difference 0.45 g,

Table 3 Summary table for two factor analysis of variance of change in condition on territory quality and throat score (see also Fig. 2)

	df	Sum of squares	Mean square	F-value	P-value
Throat score	2	0.01	0.005	2.728	0.090
Territory quality	1	0.004	0.004	1.939	0.179
Throat × territory quality	2	0.015	0.007	3.955	0.036

logistic regression $r^2=0.16$, $df =12$, $P =0.03$; Fig. 1E). Body size effects did not differ among throat colors however, indicating that large size played the same role across all throat colors in determining contest outcomes.

Of the seven usurpations that we recorded on the outcrops, all were by orange-throated males. The probability that all usurpers would have orange throats by chance alone is significantly different from random (randomization test, $P <0.04$). Because the single case in which one male usurped two territories may be considered non-independent, we removed the usurper from our randomization analysis. This result is thus a conservative one.

Contest two outcome and control plot

After the second week of territory observations we removed rock from the territories of contest winners and deposited it on the territories of contest losers (see Materials and methods). To control for the effects of rock movement between territories, we redistributed rocks within male territories on a second control outcrop. Moving rocks within a male's territory provides the same disruptive effects of rock removal, without changing thermal properties of territories per se and controls for territory shifts which may have occurred in response to changes in habitat appearance rather than quality. Similar to results from a previous study (Calsbeek and Sinervo, submitted for publication), rock manipulations on both experimental and control plots had little affect on the location of male territories before versus after the manipulations. Nearly all males (12/15) that had previously defended good territories against rivals remained on their territories even after the quality reduction. However, a small group of orange-throated males was able to regain control of the rock manipulations even after the rocks were deposited on the territories of neighbors ($n =2$ and 1 on experimental and control plots, respectively). By the end of the experiment, there was no significant difference in body size among contest winners and losers (mean difference 0.24 g, logistic regression, $r^2=0.04$, $df =12$, $P =0.33$; Fig 1F). However, throat color was still a significant factor in that orange and blue males were more likely to control good territories than were yellow males ($G^2=7.795$, $P =0.02$; Table 2).

The effect of territory quality and contests on condition

We measured a significant interaction between throat color and territory quality relating to condition (ANOVA
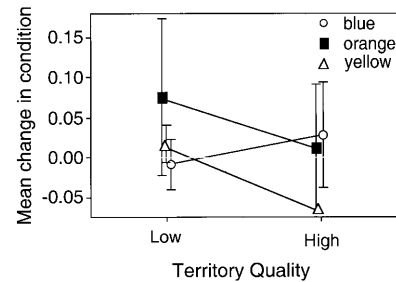
Fig. 2 Changes in condition were dependent on the interaction between throat score (*orange*, *blue*, or *yellow*) and territory quality (*high* vs *low*). Blue males on high quality territories improved in condition relative to other blue males on low quality territories. Orange males however, lost condition when on high quality territories, relative to orange males on low quality territories. This difference probably reflects the costs associated with usurping resources from other males. Because yellow males track the territorial movements of orange males (Zamudio and Sinervo 2000), yellows undergo the same loss in condition as orange males. *Points* represent a mean value for each morph (plus or minus 1 SE)

$F =3.96$, $P =0.03$; Fig. 2, Table 3). Blue males that had won contests and secured high quality territories improved in condition faster than males that lost contests and ended up on poor territories. However, orange males had lower condition after usurping territories, relative to orange males still residing on low quality territories (Fig. 2). This reduction in condition may reflect the costs of the usurper strategy employed by orange-throated males (see Discussion). Yellow males appear to suffer the same loss in condition measured for orange males, and though yellow males do not explicitly defend territories, our results show that sneaking may be physiologically costly.

Discussion

Many studies of territorial behavior have found that body-size asymmetries are the most important predictor of contest outcome (Chellappa et al. 1999; Crespi 1986; Hazlett 1968; Reichert 1982). Enquist and Leimar (1983) demonstrated theoretically that the importance of body-size asymmetry was a general principle of territorial disputes. However, an interpretation of the results from their model could not exclude the possibility that phenotypic attributes relating to dominance and aggression may be dynamic and could change over the course of the breeding season. We have presented empirical and experimental evidence of such time-dependent phenomena associated with RHP. Side-blotched lizards are an annual species

in the Coast Range, and most individuals die after a single season of reproduction. First clutch progeny hatch between May and June and mature as adults the following spring. Males and females normally become reproductively active during Mid-march and male throat colors reach full expression at this time. Thus contest one occurred after adults had become sexually mature, but prior to the onset of mating, while contest two occurred as females became sexually receptive.

Early in spring, when territory contests were first initiated, we observed a strong tendency for body size to determine contest outcome. Large males won more contests over experimental rock additions than their smaller competitors, and this difference was present irrespective of throat color. However, within 2 weeks of the first contest, we observed seven territory takeover events in which orange males that had previously lost contests moved back onto rock additions and usurped the resource from the original contest winner. Orange males also took over rock piles on our control outcrop. The usurpations on control outcrops suggest that rock movements per se are not responsible for changes in territory distributions. Although a sample size of seven observations may seem small, it is important to realize that orange-throated males are generally the rarest class of males present on the rock outcroppings (Sinervo and Lively 1996), and all usurpations that we have observed have been by orange-throated males. Moreover, we have observed the same pattern of usurping by orange males in three separate experiments (this study, Calsbeek et al. 2002; Calsbeek and Sinervo, submitted for publication) and in natural variation (Calsbeek et al. 2002).

Our results reflect the ontogeny of territoriality (Stamps 1983; Stamps and Krishnan 1998) as it relates to body size and changes in throat color. Early in spring, before throat colors had fully developed, orange males were unable to secure a high quality territory. This is likely due to the fact that androgens associated with the breeding season had yet to initiate orange-male aggression (Sinervo et al. 2000a). The strong tendency for orange-throated males to usurp resources late in the season supports our previous ideas regarding the nature of the usurper strategy (Calsbeek et al. 2002). Blue males tend to be philopatric and defend a territory very near their natal site. In contrast, orange males typically arrive on the outcroppings late in spring, far removed from their natal site (Calsbeek and Sinervo, in preparation). This suggests that orange males may assess territory quality over a larger spatial scale than do blues. The ability of orange males to take over territory space previously lost to a competitor is strong evidence that a high degree of dominance is associated with the onset of throat color expression. This is an uncommon result because prior social interactions are often thought to influence future dominance interactions (Stamps and Krishnan 1994b) and contest losers tend to remain losers in future interactions with a dominant opponent (Beletsky and Orians 1989; Kaufman 1983). The latter ideas may be inappropriate in systems with alternative male strategies in which contest outcomes change fluidly across the reproductive season as alternative tactics are expressed.

We have previously demonstrated that RHP is composed of two distinct categories of territorial behavior (Calsbeek et al. 2002). Resource defending potential (RDP) is characteristic primarily of defensive individuals who protect resources already held. In contrast, resource usurping potential (RUP) is characteristic of individuals that leave their natal site and attempt to sequester higher quality resources from other individuals. The results of the present study demonstrate that territorial behaviors of usurpers and defenders change over short time scales (e.g. within a breeding season) and that the dynamics of the two strategies are influenced differently by body size and throat color through time. While RUP and RDP have common attributes (e.g. usurpers may sequester resources but still need to defend), we distinguish the categories as discrete alternatives based on different tradeoffs associated with each (outlined below).

Physiological trade-offs

The ability of orange males to usurp territories from their neighbors is due in part to their increased fighting ability resulting from high levels of testosterone (Sinervo et al. 2000a). Orange males may have up to 50% higher stamina than either blue or yellow males (Sinervo et al. 2000a). Orange throat color also signals dominance (Sinervo et al. 2000a) and may aid in territory take-over. Defenders might lose territory to usurpers, but by sequestering more and more territory, usurpers become vulnerable to sneaker-male strategies (Zamudio and Sinervo 2000). In contrast, blue-male defenders are vulnerable to the usurping strategy of orange males, but go unchallenged by yellow sneakers (Zamudio and Sinervo 2000). Finally, the usurp strategy of orange is risky and appears to entail physiological costs of reproduction associated with high levels of testosterone (Marler and Moore 1988, 1991) that lead to elevated levels of mortality for orange males (Sinervo and Lively 1996; Sinervo et al. 2000a). This is reflected in the decreased condition of orange-throated males, but only those that sequestered high quality territory. In contrast, the defender strategy of blue-throated males appears to enhance the condition of blue males that sequestered a high quality territory. The loss of condition suffered by yellow males may result from high levels of corticosterone (Sinervo and Svensson 1998), a testosterone antagonist.

Reproductive trade-offs

Previous work in this system has shown that usurpers have a significantly higher mean and variance in reproductive success than defenders (Calsbeek et al. 2002). Differences in reproductive success are the result of differences in mortality (Sinervo et al. 2000a) and the

degree of philopatry associated with each strategy (see physiological trade-offs above). Defenders remain unable to usurp because they lack sufficient levels of testosterone to take over territories. Instead, blue males adopt a less risky mate-guarding strategy (Calsbeek et al. 2002; Sinervo and Lively 1996). Although this results in lower mean fitness for defenders, their higher survival relative to usurpers reduces the variance in defender reproductive success.

The usurper/defender dynamic could also operate in other taxa, particularly those with course resource distributions and alternative strategies. For example, marine isopods (Shuster and Wade 1992), insects (Akimoto and Yamaguchi 1997), fish (Robertson 1995), and birds (Piper et al. 2000) all show signs of similar usurping behaviors (see also Zack and Stutchbury 1992 for a review of other usurping birds). In some of these taxa (e.g. isopods; Shuster 1989) discrete alternative morphs differ in their ability to usurp and defend. Alpha-male isopods delay sexual maturity (Baitoo et al. 1988) and have higher rates of mortality than beta or gamma males, a result analogous to orange-throated usurpers in this system. In other studies however (e.g. Piper et al. 2000), the ability to usurp is linked to differences in either age or body size, demonstrating that genetically based morphs are not a prerequisite for differences in territorial behavior. In general, trade-offs associated with the usurper strategy are likely to be expressed in terms of physiological costs of fighting. Male elephant seals, *Mirounga angustirostris,* may take over females in a harem, but the efforts to do so often render males physiologically incapable of capitalizing on increased mating opportunities (D. Crocker, personal communication).

The grain of social and environmental variation has important implications for selection in neighborhoods (Levins 1962a, b), and may predict the evolution of alternative strategies (Sinervo 2001). Thus, taxa with more equitable resource distributions will likely not exhibit the same changes in territorial behavior that we have described in this study. Ultimately, the generality of this result will depend on classifying alternative types in a population and measuring temporal changes in resource use by different individuals.

The information available to contestants early in the season is limited to differences in body size. As males express more throat color, the information changes since throat color is a good indicator of stamina (Sinervo et al. 2000a). The timing of throat color display may have an associated strategic component, particularly for orange-throated usurpers, who lose in contests against yellow sneaker males and attract yellows only after the expression of their orange throats. By reserving the expression of orange-throat color until just prior to the breeding effort, orange males may be able to limit assessment (Marden and Rollins 1994) by yellow males. We suggest that a new theory may be warranted to explore the strategic consequences of delaying badge expression in systems where such a signal makes individuals susceptible to attack by alternative strategies.

Territorial behavior is one of the most well-studied aspects of behavioral ecology and many studies have successfully measured several important aspects of aggression and spacing behavior (Brown 1964; Brown and Orians 1970; Davies and Hartley 1996; Fox et al. 1981; Stamps 1994). However, territoriality and aggression have proven to be extremely difficult behavioral traits to measure in the wild (Davies and Houston 1978; Maher and Lott 1995; Stamps and Krishnan 1995). This is in part because contests often occur very quickly and may rarely be observed (Piper et al. 2000). Previous studies of territoriality have relied heavily on RHP as a measure of dominance in field studies. RHP describes intrinsic differences among individuals that lead to asymmetric contest outcomes and is a useful system for descriptive behavioral work. However, our results suggest that RHP is not a singular quality and may be better understood in the context of alternative tactics to the same end. We have demonstrated that resource usurping and resource defending potential are informative components of RHP for measuring different aspects of territoriality. Moreover, our demonstration that body size and throat color play changing roles over the course of the breeding season, outlines a clear ontogeny of territoriality as lizards undergo a striking maturation process. We suggest that a clearer understanding of territoriality will require field experiments in which important ecological resources are manipulated, and traits like aggression and territoriality are measured repeatedly over the course of the breeding season (Arnold and Wade 1984). Finally, we point out that RUP and RDP may well govern territorial interactions between males in other taxa with continuous differences in testosterone. The dichotomous nature of morphs in this system simplifies their detection.

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