Behavioral attributes influence annual mating success more than morphological traits in male collared lizards

Troy A. Baird, John M. Hranitz, Dusti K. Timanus, and Andrew M. Schwartz

Traits that potentially influence mating success (MS) may be “static” with low lability once they develop or “dynamic” with highly modifiable expression. We used principal components (PCs) analyses of dynamic behavioral and morphological traits that are static over the short term to determine their relative contributions to the ability of territorial male collared lizards to acquire access to females and obtain high MS. We estimated annual MS of males as the relative frequency with which they engaged in courtship with reproductively active resident females. Three PCs explained statistically significant phenotypic variation among males. Morphological traits loaded significantly on 2 PCs that explained 26.3% and 13.0% of the variance, respectively, whereas behavioral variables loaded significantly on a different component that explained 15.7% of the variance in male traits. The frequency with which males initiated aggressive encounters with same-sex competitors did not load significantly on these PC axes. Males having behavioral PC scores above the mean had significantly higher MS than those with behavioral scores below the mean, whereas male MS was not related to component scores for either of the axes describing static morphological variables. Results indicate that in our population behavior patterns associated with advertisement, particularly to females, influence male MS more strongly than morphological traits or the initiation of direct aggression with same-sex competitors.

Key words: behavior, collared lizard, mating success, morphology.

Mating success (MS) is an important component of individual fitness (Vehrencamp and Bradbury 1984; Clutton-Brock 1988). Especially in polygynous species under strong sexual selection, males achieve high MS by maximizing the number of females that they encounter and court (Andersson 1994; Whiting et al. 2003). As a consequence, phenotypic traits that promote the ability of males to compete for and/or attract mates are often under strong selective pressures (Endler 1986; Andersson 1994; Andersson and Iwasa 1996). In many species, males garner access to multiple mates by defending breeding territories that contain one or more resources that females require for reproduction (Emlen and Ovington 1977; Stamps 1994; Kwiatkowski and Sullivan 2002). Because the number of females that males can access may vary markedly as a function of territory area (Hixon 1987; Davies 1991) and/or quality (Walls et al. 1989; Hews 1990; Mathis 1991; Hews 1993), the resultant polygynous mating systems are often characterized by large within-population variance in the MS of males (e.g., Howard 1988; Warner and Schultz 1992). Therefore, phenotypic traits that promote success in intrasexual contests over breeding territories and/or attract females are particularly interesting to measure because they may lead to large mating asymmetries among males (Clutton-Brock 1988; Kingsolver et al. 2001).

Many investigations have focused on the role of morphological features that are not usually modified by males over the short term (static characters, sensu Hill et al. 1999) in the ability of males to achieve high MS. Large total body size (e.g., Clutton-Brock et al. 1979; Howard 1988; Hews 1990) and enlarged structures have been linked to high male MS (e.g., Vitt and Cooper 1985; LeBas 2001). These traits may function as armaments in intrasexual contests (e.g., Berglund et al. 1996; Bull and Pamula 1996; Hagelin 2002; Whiting et al. 2003), may be honest signals of resource holding power (Husak 2004), and/or may function as ornaments that attract mates (Biscoff et al. 1985; Basolo 1990a, 1990b; von Shantz et al. 1994; Rintamäki et al. 2000). Similarly, conspicuous coloration (sometimes including ultraviolet reflectance) may also promote high male MS (Thusius et al. 2001; Lappin et al. 2006) either through attraction of females (Price 1984; Järvi et al. 1987; Höglund et al. 1990; Smith et al. 2002) or by promoting song quality and attractiveness to other males (Gerald 2001; Pryke et al. 2001; Whiting et al. 2003). Although static traits may promote male success in some species, they may not influence mating opportunities to the extent that labile behavioral traits do. Hence, the target of selection may be the extent to which individuals maximize their use of highly labile behavioral traits and/or use their maximal capacity to perform physically (e.g., sprint fast, exert bite, or claw force), given the underlying limitations imposed by static physical attributes (Sneddon et al. 2000; Huyghe et al. 2005; Lalivaux et al. 2005; Lappin and Husak 2005; Husak et al. 2006).

Consistent with this hypothesis, the phenotypic traits that correlate best with high male MS in many species are often behavioral attributes that males can modify over the duration of individual interactions with conspecifics (dynamic traits, sensu Hill et al. 1999). Such behavioral traits may modulate the relationship between maximal performance and fitness among males at similar times in growth and development (Garland and Losos 1994; Irschick and Garland 2001; Husak et al. 2006). Highly successful males sometimes engage in agonistic contests with competitors more frequently (McElligott
We tested the extent to which morphological (static) and/or behavioral (dynamic) attributes were important for obtaining high MS in territorial male eastern collared lizards, *Crotaphytus collaris*. This is a good model system for such a test because further growth and development of morphological traits is minor once males acquire territories (Baird, Timanus, et al. 2003; Baird and Hews 2007). Consequently, our study compares behavioral traits (dynamic) when the morphological phenotype is fully developed. Previous field studies have documented the social structure in our study population characterized by male defense of breeding territories (reviewed by Baird, Timanus, et al. 2003). Territory defense sometimes involves fighting, and both bite force and sprint speed have been positively correlated with MS in 2 other Oklahoma collared lizard populations (Lappin and Husak 2005; Husak et al. 2006; Peterson and Husak, 2006). Moreover, displays given during staged aggressive encounters between males in these populations have been hypothesized to function as honest signals to rival collared lizard males of the ability/willingness to attack aggressively (Husak 2004), and gaping displays are suggested to advertise male bite force (Lappin et al. 2006). In our population, aggressive contests between males that involve physical contact occur very infrequently and are almost always resolved without biting or other contact (Baird et al. 1996; Baird, Timanus, et al. 2003). Instead, males invest large amounts of time and energy displaying when they are not interacting with conspecifics of either sex, but displays can be seen readily by both male rivals and females (Baird et al. 1996; Baird, Timanus, et al. 2003). Because displays given at a distance can potentially signal either male rivals or females, relationships between static and dynamic male attributes that may function in advertisement and MS merit further investigation in collared lizard males.

As a consequence of their heavy investment in advertisement (Baird et al. 1996; Baird, Timanus, et al. 2003), we predicted that dynamic behavioral traits would play a more important role in male MS than static morphological traits. We tested this prediction using PCA to characterize trait variation among collared lizard males and then tested for main and interactive effects of suites of traits (PCs) on annual male MS that we estimated from focal observations detailing the proportion of courtship interactions that females entered with each male (Baird et al. 1996; Baird, Timanus, et al. 2003; Lappin and Husak 2005; see below).

### METHODS

#### Study subjects and general methods

At the Arcadia Lake (AL) Dam, 9.6 km east of Edmond, Oklahoma County, OK, *C. collaris* occupies 3 topographically homogeneous patches of boulders (1505–19 853 m²) imported to construct flood-control spillways. This site is optimal for behavioral studies because human access is restricted, lizards are undisturbed, we know the ages of all the males from mark-recapture studies conducted since 1990, and the homogeneity of this habitat allows prolonged and unobstructed view of all lizards (Baird et al. 1996; Baird, Timanus, et al. 2003). Beginning when they were hatchlings, lizards were noosed, the terminal phalanges of 3 digits clipped for permanent identification, and unique combinations of nontoxic acrylic paint spots applied to the dorsum for identification from a distance.

By the beginning of the second activity season (April–August), males attain a snout-vent length (SVL) of at least 100 mm at which point growth slows (Baird, Timanus, et al. 2003). Most (>95%) males acquire a territory at the beginning of their second season (hereafter 2y + males) that they defend each subsequent season until they die (Baird et al.

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<td>3. Morphology - Behavior -</td>
<td>4. Morphology + Behavior -</td>
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**Figure 1**

Hypothetical 2-factor model depicting how suites of morphological (M) and behavioral (B) attributes may influence male MS. The model generates 4 unique predictions about the MS of males expressing morphological or behavioral traits above and below the mean values. Hypothesis A; main effect of M, no interaction between M and B; predicted male MS ranking: 4 = 2 > 1 = 3. Hypothesis B; main effect of B, no interaction between M and B; 1 = 2 > 3 = 4. Hypothesis C; main effect of M with interaction between M and B; predicted male MS ranking; 2 > 4 > 1 > 3. Hypothesis D; main effect of B with interaction between M and B; predicted male MS ranking; 2 > 1 > 4 > 3.

and Hayden 2000) and perform visual displays with high frequency (Holmberg et al. 1989; Kodric-Brown and Nicoletto 2001), greater intensity (Kodric-Brown 1995; Enstrom et al. 1997), or longer duration (Arak 1983; Gerhardt et al. 2000). In other cases, the most successful males are those that acquire territories that are larger (Keyser and Hill 2000; Zamudio and Sinervo 2003; Husak et al. 2006) and/or contain high quality resources that are critical to females (Alatalo et al. 1986; Kraak et al. 1999). Independent of resources, females may be attracted to males that perform displays that are more conspicuous, perhaps, because these advertise genetic fitness that will be inherited by the female’s offspring (von Schantz et al. 1994; Andersson and Iwasa 1996).

Because multiple traits that promote high reproductive success are often integrated (Lande and Arnold 1983; Candolin 2005), it may be difficult to determine the relative contributions of specific individual attributes to the success of males (Zuk 1991; Kodric-Brown and Nicoletto 2001; Künzler and Bakker 2001). Suites of static morphological and dynamic behavioral attributes that hypothetically influence male reproductive success can be characterized by multivariate methods such as principal components analysis (PCA) that partition variation among orthogonal, statistically significant axes standardized to a mean of zero (Figure 1). A graph of scores on 2 such principal components (PCs) axes partitions variation as suites of related traits that can then be tested for relationships with male MS. If variation in individual PCs explains patterns of MS, then the success of males with scores above the mean for those components should be higher than the success of males having scores below the mean, independent of scores on other PCs. One possibility is that morphological and behavioral traits segregate on separate PC axes (Figure 1, Hypothesis A or B). However, it is also possible that significant PCs are combinations of morphological and behavioral traits that may influence MS. This approach can also be used to test whether or not suites of traits (PCs) have interactive effects, in which case the distribution of male MS is expected to vary depending upon the relative importance of the suites of correlated attributes (Figure 1, Hypotheses C and D).
Territories are defended against neighboring territory owners as well as nonterritorial first-year males primarily using patrol and display punctuated by occasional chases, and much more rarely by overt aggression involving biting (Baird et al. 1996; Baird, Timanus, et al. 2003; Husak 2004). Male territories at least partially overlap the home ranges of up to 8 females that males interact with throughout the 2.5-month (May 1–July 15) reproductive season using intimate physical contact and display patterns that are visually conspicuous (Baird et al. 2001; Baird 2004). Although nonterritorial first-year males become sexually mature at 72-mm SVL, we restricted our study to 2y + males. First-year males court females only infrequently; females usually flee first-year males, although they participate in prolonged courtship interactions with 2y + males, and first-year males immediately flee when they encounter territorial 2y + males (Baird et al. 1996; Baird and Timanus 1998). Moreover, microsatellite studies of paternity both at AL (Hranitz JM and Baird TA, in preparation) and at another central Oklahoma location (Husak et al. 2006) confirm that 2y + males sire the majority of the hatchlings in these populations. In all years, we recorded data on all the 2y + males present on the site but excluded 2 males because they survived less than one-half of the reproductive season. By contrast, 2 other males held the same territories during all 4 seasons of this study. To avoid pseudoreplication, we randomly selected data from one season for these 2 males. Using these criteria, we analyzed data on a total of 37 males (90% of territorial males present) ranging in age from 2 to 5 years (1997, N = 13; 1998; N = 7; 1999, N = 8; 2000, N = 9). Because Bartlett’s tests revealed homogeneity among variances, we pooled data from different years.

**Morphometry**

We measured morphometric traits thought to be under sexual selection in *C. collars* and/or other lizards (Cooper and Vitt 1993; McCoy et al. 1994; Baird, Vitt et al. 2003) or are potentially related to display patterns in male collared lizards (Carpenter and Ferguson 1977; Baird et al. 1996; Husak 2004). Morphometrics were recorded in the field on May 10–15 in all years. These included SVL, tail length (vent to tip of the snout), maximum head width (at the jaw articulation), and fore- and hindleg length from the proximal insertion to the tip of the longest digit on the right side. All morphometrics were recorded to the nearest 0.5 mm using either a ruler or calipers. We recorded body mass to the nearest 0.5 g using a spring scale (Pesola). Because body symmetry may influence MS in sexually selected species (Thornhill and Møller 1998), we also determined the difference between the number of femoral pores on the right and left hindlegs as an estimate of fluctuating asymmetry (Møller and Swaddle 1997). We omitted male age from analyses because once males acquire a territory during their second year, frequencies of territorial behavioral patterns were not related to age (Schwartz et al. 2007) and male growth slows markedly at age 2 years (Baird, Timanus, et al. 2003) that is the minimum age of males used in this study.

**Chroma**

We recorded color measurements in the field on sunny days when substrate temperatures and lizard cloacal temperatures were 34–40 °C. We used the *Munsell Color Chart for Plant Tissues* (Munsell 1969) to match the colors of the dorsal, dorsolateral, ventral–lateral, gular, and dorsal fore- and hindleg dorsal surfaces (see similarly Baird et al. 1997) but eliminated gular coloration because measurements showed almost no variation. Less than 6% of the color reflectance from these body areas in *C. collars* falls within ultraviolet spectra (McCoy et al. 2002, 2004). Therefore, these charts give a valid measure of color in this species. The Munsell chart identifies the quality by which one color is distinguished from another (hue), the lightness or darkness of a color (value), and color saturation (chroma) (Munsell 1969; Zucker 1988). Although the hue (primarily green and yellow) of *C. collars* males, including those in Oklahoma, varies geographically (McCoy et al. 1997; Macedonia et al. 2004), both hue and value among AL males showed little variation (coefficients of variation for color measurements from different body areas; hue = 0.107–0.134; value; 0.100–0.171). Because variation in chroma was much higher among AL males (coefficients of variation 0.966–0.603), we used only chroma values in statistical analyses.

**Behavior**

We recorded all social and spatial data on scale-drawn maps of the study site. Maps were prepared using markers placed in a grid over the site, the locations of which were then measured (± 1 m) using US Air Force Global Positioning Satellite equipment (Baird and Timanus 1998). Behavioral data were recorded when substrate temperatures were 30–38 °C, a range which is optimal for collared lizard social activity (Baird et al. 1996) and over which lizard activity is independent of surface temperature (Baird et al. 2001). We recorded on maps focal individual observations (sensu Altman 1974) during which we traced the travel path of males from perch to perch, all social displays initiated, and the identity of all lizards involved in intra- and intersexual proximal encounters (defined below). Social displays are initiated by AL males in 2 distinct contexts (Baird et al. 1996; Baird, Timanus, et al. 2003). Distant social acts are by far the most common in AL males (Baird et al. 1996). These are displays performed by patrolling males while they paused on elevated perches that were more than 5 m from the nearest conspecific, and these behaviors did not evoke a response (i.e., retreat, approach, and display) from another lizard. Most (98%) of the distant displays given by AL males are lateral compression of the torso while the dewlap is extended, up and down movement of the head only (head bob), and up and down movement of the entire body by flexing the legs (push-ups). Less frequently (2%), males walk in circle or figure-8 patterns. In contrast with distant displays, proximal aggressive encounters were characterized by the focal male closing to within 1 m of another male that evoked a response (display, attack, and flight) from the other male (Baird et al. 1996). Proximal encounters were considered terminated when the participants separated and began other activities (patrolling and foraging).

We recorded 300 min of focal observations per male (fifteen 20-min observations) on 15 different days throughout the reproductive season (May and June) over which time females produce 1–3 successive clutches and 2y + males actively defend their territories (Baird et al. 2001; Schwartz et al. 2007). Frequencies of male behavior do not vary as a function of time of day from 900 to 1300 h when we recorded focal observations (Baird et al. 2001). However, to eliminate any possible bias during this 4h time period, we observed individual males each day in random order. For each male, we calculated hourly frequencies of displays and encounters by dividing the total number of these acts/events by the total observation time on these individual males. We measured mapped focal traces using a digital planimeter (Planix 2000) and calculated the rate of male patrol by dividing the total distance traveled by the total observation time for these males (Baird et al. 1996).
In addition to focal observations, we recorded point sightings on maps during routine censuses of study sites. We recorded over 200 censuses daily, with dual daily censuses being separated by at least 1 h, and a second daily location was recorded for males only if they had moved at least 5 m since the previous census. Point location sightings for each male were combined with the beginning and ending points from each male’s focal traces (x number of points = 62.8 per male, 1.0 standard error = 2.5) to construct territory maps using the minimum convex polygon technique (Turner 1971).

The number of points that we used to construct the composite maps (60–65) exceeded the number necessary to achieve an asymptotic relationship when we graphed territory area versus the number of sightings (Stone and Baird 2002), following the method of Rose (1982). We measured territory area from composite maps based on census and focal observations using a digital planimeter.

**Estimates of annual male MS**

We estimated annual male MS using the proportion of courtship encounters initiated by males during focal observations and censuses (Clutton-Brock et al. 1982; Baird et al. 1996; Lappin and Husak, 2005). We included as potential mates only females that were known to produce at least one clutch of eggs as determined by abdominal palpation (x interval between palpations = 14 d). Courtship encounters in *C. collaris* at AL are conspicuous interactions lasting from 2 to more than 30 min and involve various forms of physical contact (described below) as well as the exchange of displays (described above) while the male and female remain within one body length of one another (Baird 2004). We tallied as courtship encounters only instances when both the female and the male participated and eliminated the very few instances when females moved away or hid when 2y + males approached (Baird and Timanus 1998). Courtship encounters began when males approached and performed displays (described above) when they were within one body length of the female. In most (95%) instances, females responded to approaching 2y + males by extending their dewlap and raising their hindlegs, cloacal area, and proximal tail while keeping the distal portion of the tail on the substratum (female greeting display [Baird 2004]). At this point, physical contact occurred, which could include the male mounting the female’s dorsal surface and attempting to juxtapose his vent with her’s (attempted copulation), either lizard sitting upon the dorsal surface of their partner without juxtaposition of the vents, superimposition of the legs and/or tails, nudging their partner with the snout, or perching adjacent to while touching their partner (Baird and Sloan 2003; Baird 2004). Courtship encounters occurred throughout the reproductive season regardless of female reproductive condition and involved many acts other than attempted copulation. These observations suggest that courtship promotes the formation of social bonds that almost certainly play an important role in mating relationships. We did not use attempted copulations alone to assign mating partnerships because it was not possible to determine which events resulted in successful intromission and we observed many male and female pairs to engage in multiple, prolonged courtship encounters during which we did not observe attempted copulation.

We calculated annual MS using the relative frequencies of courtship encounters initiated by each male with all mature females present. For each female, we determined the proportion of her total courtship encounters with each male (for most females 100% with one male, see below) and considered this proportion his MS with that female. We then summed these proportions to estimate the total MS (number of females for each male) for each male (Baird et al. 1996; Lappin and Husak 2005). Most (92.7%) of the females in our study were courted by only one male, the male whose territory overlapped that female’s home range. The remaining 7.3% were courted by 2 males. Although the home ranges of these females overlapped mostly with one male’s territory, they extended partially into the territories of one other neighboring territorial male. In these few females that were courted by 2 territorial males, there was a strong bias for courtship by one of the males, 70% versus only 30% with the second male. This estimate of MS allows for the possibility that clutches of *C. collaris* females may be fertilized by more than one male, which has been documented in other lizards (Abell 1997). The fact that we observed a strong bias in the relative frequency that females were courted by the same (overlapping) male throughout the reproductive season suggests that the relative frequency of courtship is a strong correlate of mating relationships between individual males and females, and this same technique has been used in other studies to estimate MS in male collared lizards (Baird et al. 1996; Baird, Timanus, et al. 2003; Lappin and Husak 2005).

**Principal components analyses**

We performed PCAs on a correlation matrix, using the varimax rotation procedure to reduce the dimensions of the morphological and behavioral variables to a smaller number of synthetic components (Pimentel 1979). Such PCs are statistically independent linear combinations of the original variables (Dautrey 1976; Flury and Riedwyl 1988; James and McCulloch, 1990; Jackson 1991). PCA requires at least 2 replicate data points (in this case males) per measured variable (Pimentel 1979), which is satisfied in our sample (N = 37 males, N = 17 variables). We included in the PCA, SVL, tail length, body mass, head width, head length, length of the fore-, and hind-limbs, difference between the number of femoral pores on the right and left hindlegs, chroma measures from the dorsal, dorsal lateral, and ventral lateral body as well as the dorsal surfaces of the proximal fore- and hindlegs, territory area, and rate of patrol (m/h), the hourly frequencies of distant displays (those not given during proximal encounters), and male–male encounters initiated (see above). Because we measured the relative contribution of morphological and behavioral variables to male MS, we excluded our estimates of MS from the PCA.

We considered statistically significant only PCs with eigenvalues that exceeded those predicted by the broken stick model (Legendre and Legendre 1983; Jackson 1993). We identified statistically significant contributions of individual variables to statistically significant PCs using the bootstrapped broken stick method (Peres-Neto et al. 2003). Using 1000 bootstrapped samples, we ascertained that the 95% confidence interval included the values expected under the broken stick model and estimated the P value as the number of bootstrapped samples greater than or equal to the broken stick values (Peres-Neto et al. 2003). For all PCs that exceeded the broken stick model criteria, we classified males according to whether their scores were above or below the mean and compared the annual MS of males in these groups using 3-factor analysis of variance (ANOVA). We also calculated a 3-factor regression on male MS with interaction terms for PC1, PC2, and PC3.

Both the relative abundance of potential mates and competitors (other mature males) where males establish territories may also influence both the ability of males to monopolize females and the costs of territory defense (Hixon 1987; Zamudio and Sinervo 2003). Therefore, the social behavior of males in our population could also be influenced by these environmental variables, and male morphological
attributes may influence their ability to compete under different densities of competitor males. To examine these possible factors, we used census sightings to calculate the density of females and the density of competitor males on each 2y+ male’s territory. Competitor males included the 2y+ males occupying neighboring territories (2–3 neighbors) plus sexually mature first-year males that use stealthy subordinate tactics to live within the boundaries of 2y+ male territories and attempt to pilfer copulations with females (Baird and Timanus 1998). We calculated the densities of females and competitor males (separately) by dividing the number of lizards sighted within and bordering each male’s territory, by territory area. For each PCA factor that exceeded broken stick model criteria (see above), we grouped our 2y + males according to whether their factor scores were above or below the mean and compared the density of females and the density of competitor males (separate analyses) on the territories defended by these males using 3-way ANOVA.

RESULTS

Only the first 3 PCs explained significant trait variation among males in the broken stick model. Together, these PCs explained 55% of the total variance in male traits. Individually, PCs 1–3 explained 26.3%, 15.7%, and 13.0% of total male variation, respectively. With the exception of hindleg length loading significantly on both PC1 and PC2 (highest loading on PC1, Table 1), all other traits loaded significantly on only one of PCs 1–3. Six of 8 variables that loaded significantly (P < 0.05) on PC1 were male size traits, whereas the other 2 were chroma, one of which had a negative loading (Table 1). Only behavioral variables associated with male advertisement and occupancy of territories (3 of the 4 that we measured) loaded significantly on PC2. Femoral pore difference, chroma on the dorsum, and fore- and hindlegs loaded significantly on PC3. Two of the variables that we measured (tail length and frequency of male aggressive encounters) did not load significantly on the first 3 statistically significant PCs (variables indicated by italics in Table 1).

Thirteen of 17 males (76.4%) with MS scores above the mean had positive PC2 scores compared with 9 of 17 (52.7%) having positive PC1 scores (Figure 2). Neither PC1 (F1,29 = 1.29, P = 0.265) nor PC3 (F1,29 = 0.956, P = 0.336) were significantly different for males having MS estimates above and below the mean (Figure 3). By contrast, there was a main effect of PC2 (F1,29 = 8.40, P = 0.007) with males having PC2 scores above the mean obtaining higher MS than males with PC2 scores below the mean (Figure 3). There were no interactive effects (P > 0.05) among the 3 PCA factors on male MS. Similarly, 3-factor regression of PC scores against male MS revealed a significant overall effect (r² = 0.409, F1,29 = 2.87, P = 0.006), with PC2 being the only significant main effect (t = 4.17, P < 0.01) and no interactive effects.

We compared the number of females and the number of same-sex competitors (separate 3-way ANOVAs) for males grouped according to whether their PC1–PC3 scores were above or below the mean. The density of females on male territories did not differ between males grouped according to scores on PC1 (F1,29 = 1.00, P = 0.325), PC2 (F1,29 = 0.153, P = 0.699), or PC3 (F1,29 = 0.248, P = 0.622) or males grouped in interactive effects among PC1–PC3. Similarly, the density of male competitors on male territories did not differ between males grouped according to scores on PC1 (F1,29 = 1.00, P = 0.325), PC2 (F1,29 = 0.153, P = 0.699), or PC3 (F1,29 = 0.248, P = 0.622) or males grouped in interactive effects among PC1–PC3. Thus, males with higher MS were not associated with increased densities of females or of same-sex competitors on their territories.

DISCUSSION

Our results show that a suite of 3 dynamic behavioral traits described by PC2 are positively related to the MS of territorial AL males more than static morphological and chroma traits. By contrast, aggressive contests between males were infrequent in our population, and the frequency of aggressive encounters initiated did not load significantly on PC2 or the other 2 statistically significant PCs. Because the most prominent activity of territorial collared lizards consists of movements among perches as they patrol and then pause to perform displays (Baird et al. 1996, 2001; Baird, Timanus, et al. 2003), it is not surprising that rates of patrol and distant display were related. Also, patrol rate was likely related to territory area because larger areas would require males to cover more distance. Display and patrol behavior likely allow effective signaling of conspecifics from a distance because collared lizards have highly developed vision and their conspicuous displays

Table 1

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1 (26.3%)</th>
<th>PC2 (15.7%)</th>
<th>PC3 (12.9%)</th>
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<tr>
<td>SVL</td>
<td>0.888 (78.85)</td>
<td>0.046 (0.21)</td>
<td>0.127 (1.61)</td>
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<td>Mass</td>
<td>0.874 (76.39)</td>
<td>-0.0002 (0.0004)</td>
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<td>Head width</td>
<td>0.590 (34.81)</td>
<td>0.283 (8.00)</td>
<td>-0.227 (5.15)</td>
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<td>Head length</td>
<td>0.859 (76.39)</td>
<td>0.136 (1.85)</td>
<td>-0.191 (3.65)</td>
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<td>Foreleg length</td>
<td>0.719 (15.06)</td>
<td>-0.245 (6.00)</td>
<td>0.105 (1.10)</td>
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<td>Hindleg length</td>
<td>0.740 (54.76)</td>
<td>-0.528 (27.87)</td>
<td>0.173 (2.99)</td>
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<td>Tail length</td>
<td>0.121 (1.46)</td>
<td>0.092 (0.85)</td>
<td>0.213 (4.54)</td>
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<td>Femoral pore difference</td>
<td>-0.101 (1.02)</td>
<td>0.187 (3.50)</td>
<td>-0.346 (11.97)</td>
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<td>Territory area</td>
<td>-0.079 (6.24)</td>
<td>0.734 (53.88)</td>
<td>0.295 (8.70)</td>
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<td>Patrol rate</td>
<td>-0.114 (1.30)</td>
<td>0.887 (78.68)</td>
<td>0.103 (1.06)</td>
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<td>Distant displays/h</td>
<td>0.057 (3.25)</td>
<td>0.304 (64.64)</td>
<td>-0.191 (3.65)</td>
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<td>Male-male encounters/h</td>
<td>-0.097 (0.94)</td>
<td>-0.094 (0.88)</td>
<td>0.215 (4.62)</td>
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<td>Dorsal chroma</td>
<td>0.060 (0.36)</td>
<td>0.032 (0.10)</td>
<td>0.685 (46.92)</td>
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<td>Dorsal-lateral chroma</td>
<td>0.359 (12.89)</td>
<td>-0.001 (0.0001)</td>
<td>0.208 (4.33)</td>
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<td>Ventral-lateral chroma</td>
<td>-0.474 (22.47)</td>
<td>0.241 (5.81)</td>
<td>0.425 (18.06)</td>
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<td>Foreleg chroma</td>
<td>0.002 (0.0004)</td>
<td>-0.324 (10.50)</td>
<td>0.692 (47.89)</td>
</tr>
<tr>
<td>Hindleg chroma</td>
<td>-0.149 (2.22)</td>
<td>0.270 (7.29)</td>
<td>0.689 (47.47)</td>
</tr>
</tbody>
</table>

Parenthetical numbers beneath the column headings are the total variation explained by each factor. Boldface indicates the statistically significant loadings for each variable. Variables that are italicized did not have statistically significant loadings on PCs 1–3.
transmit well throughout their open, rocky habitats. Frequent distant display may be advantageous because it is an effective means of intra- and intersexual signaling that does not carry the high costs associated with direct aggression (Marler and Moore 1988, 1989, 1991; Marler et al. 1995). Male collared lizards appear to reduce defense costs by modifying their social behavior in several ways, including decreased use of costly attacks on intruders as males gain experience (Schwartz et al. 2007), reducing the intensity of responses to intrusions by familiar neighbors (Fox and Baird 1992; Husak and Fox 2005), and by establishing territories at the beginning of the reproductive season without frequent aggression with same sex conspecifics (Baird et al. 2001). Together, these results suggest that frequent engagement in direct intrasexual aggression may act antagonistically with patrol and distant display, which appear to be important for advertisement to females and promoting high MS.

Although large body size was not a strong predictor of male MS, it is clearly a requirement for acquisition of a breeding territory in the AL population (Baird et al. 1996; Baird, Timanus, et al. 2003). Unless larger males are absent as a consequence of predation or overwinter mortality (Baird and Timanus 1998; Baird TA and Curtis JL, in preparation), smaller first-year males that are sexually mature do not acquire territories until their second season when they are large enough to compete (Baird et al. 1996; Baird, Timanus, et al. 2003). Although a minimum size is necessary to qualify as an effective competitor and both bright coloration and large size promoted success in staged laboratory contests between AL males (Baird et al. 1997), these are all traits that males cannot modify during individual social encounters and they were not strong correlates of high mating male MS in the field (Baird et al. 2003; Lappin and Husak 2005; results in this study). Instead, dynamic traits that can be modified over the short term, indeed rapidly, correlated best with high MS in the AL population.

The selective landscape for male attributes that promote male MS may show substantial interpopulation variation in collared lizards because they are restricted to patches of rocky habitat among which there is limited gene flow (Hranitz and Baird 2000). Indeed, males from 3 Oklahoma populations (including AL) differed in the degree of sexual size and color dimorphism (McCoy et al. 1994, 1997; Macedonia et al. 2004), and laboratory studies revealed interpopulation differences in the roles of both male size and coloration in staged male–male contests and female choice trials (Baird et al. 1997). Using males from yet other Oklahoma populations, male sprint speed and bite force were positively correlated with field estimates of male MS (Lappin and Husak 2005; Husak et al. 2006; Peterson and Husak 2006). Both performance traits may be important in male aggressive contests that were suggested to be much more frequent in these study populations than we observed in the AL population. Therefore, although behavioral attributes were more important determinants of high MS than morphological traits in the AL population, different combinations of male traits may be important in other populations. Possible interpopulation variation in the relative importance of phenotypic traits in male collared lizards merits further investigation.

Numerous studies on diverse vertebrates have reported that static morphological, primarily size-based characters are important determinants of male MS (reviewed by Andersson 1994). Body size–independent morphological performance traits are also linked to male MS (Lappin and Husak 2005; Peterson and Husak 2006), but the manner in which such traits are related to variation in male fitness remains less clear (Garland and Losos 1994; Irshick and Garland 2001). Our results add to a growing body of evidence that male MS, and ultimately fitness may be modulated by traits that males can change rapidly in response to labile social conditions/opportunities. In some species, such dynamic traits may include badges of status involve whole body coloration that can be changed rapidly (i.e., during individual social interactions; Greenberg and Jenssen 1982; Greenberg and Crews 1983; Zucker and Murray 1996), whereas in others, males can modify the shape, size, and color of specific ornamental structures (e.g., head combs, Rintamäki et al. 2000; head plumage, Hagelin 2002). Perhaps because displays that are not dependent on body size are especially amenable to rapid modification of frequency and intensity, male success is linked to behavior patterns that function via competition with same-sex rivals and/or female choice. Although in some fishes and birds, static morphological traits appear to be necessary “qualifying” characters (Houde 1997; Kodric-Brown and Nicoletto 2001), females prefer to mate with males that display more frequently
or vigorously (Holmberg et al. 1989; Hill et al. 1999; Carvalho et al. 2005). Similarly, some female anurans prefer males that give either longer (Gerhardt et al. 2000) or more frequent vocal displays (Wagner and Sullivan 1995). Male deer attain dominant status through both frequent intrasexual aggression and vocal display (McElligott and Hayden 2000; McElligott et al. 2001), and behavioral traits appear to be more important than size for obtaining high MS in male wood rats (Topping and Millar 1999). We suggest that territorial collared lizard males alter dynamic behavioral attributes depending upon the immediate opportunities for courtship and the challenges posed from same-sex competitors and that such dynamic behavioral attributes may play an important role in determining the MS of individual males.

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ABBREVIATIONS


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