
DEMOGRAPHIC ASSESSMENT OF THE TRIPLOID PARTHENOGENETIC LIZARD *ASPIDOSCELIS NEOTESSELATUS* AT THE NORTHERN EDGE OF ITS RANGE

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Abstract.—*Aspidoscelis neotesselatus* (Colorado Checkered Whiptail) is a hybrid-derived triploid parthenogenetic lizard with a natural range overlapping with six counties in southeastern Colorado, USA. It has also become established by anthropogenic causation in Grant County, Washington State, approximately 1,600 km northwest of its range in Colorado. Large parts of its natural range are within military reservations. Reduced genetic variation in all-female species makes them especially susceptible to environmental disturbances, such as military activities. At Fort Carson (FC), we estimated an abundance index via a catch-per-unit estimator, weekly survival using Cormack-Jolly-Seber models, and body condition and clutch size as indicators of population health across three low-impact training areas (TA; 45, 48, and 55). Abundance estimates varied across TAs from a low of 0.99 to a high of 6.12 females per hectare. Body condition only marginally varied by age class and TAs. Apparent monthly survival was relatively low in all areas and even lower at TA 55 than at TA 48 (0.638 versus 0.771); however, the uncertainty around those estimates was large. Results suggest that TA 48 supported a large fraction of reproductive females that were successful in producing eggs, providing further insight into where monitoring and conservation efforts should be concentrated within FC.

Key Words.—abundance; body mass; catch-per-unit effort; conservation; demography; survival; whiptail

INTRODUCTION

Aspidoscelis neotesselatus (Colorado Checkered Whiptail; Fig. 1) is a hybrid-derived triploid parthenogenetic species. It was described by Walker et al. (1997a) from the then known four-county range in southeastern Colorado, USA; however, subsequent reports have redefined the range to include Teller and El Paso counties (Taylor et al. 2015a), as well as new sites discovered in Las Animas (Taylor et al. 2006a), Pueblo (Taylor et al. 2006b; Susan Spackman Panjabi et al., unpubl. report), Fremont (Taylor et al. 2015b), and Otero (Walker et al. 2012; Taylor et al. 2015b; Taylor 2016) counties. It has also become established by apparent anthropogenic causation in Grant County, Washington, USA, about 1,600 km northwest of its natural range in Colorado (Weaver et al. 2011). This triploid species resulted from hybridization between diploid normally parthenogenetic *A. tessellatus* and gonochoristic *A. sexlineatus*, most likely in the Purgatoire River Valley in either Las Animas or Otero counties. Its range expansion has occurred from the site of origin, via the descendants of a single hybrid individual (Parker and

Selander 1976), as they spread from within or from zones of syntopic contact with either one or both progenitors (Walker et al. 1997a; Taylor et al. 2006a,b; 2015a,b). During this process, *A. neotesselatus* has diversified into four distinctive allopatric variants, referenced as pattern classes A, B, C, and D (Walker et al. 1997a, 2012), within a unisexual mode of reproduction. There is a variant of the species at Fort Carson, Colorado, that is described as pattern class A (Walker et al. 1997a; Taylor et al. 2015a).

The reduced genetic variation of this parthenogenetic species could make it susceptible to environmental disturbances; however, parthenogenetic species as a group often inhabit areas devoid of gonochoristic congeners (Wright and Lowe 1968). In addition, the weed hypothesis and field observations support the idea that unisexual whiptails are adapted to disturbed areas that are not optimal for sympatric bisexual species, given unisexual species the ability to proliferate fast, just as would plant weeds found primarily in such disturbed areas (Baker 1974). The species, however, has had multiple conservation listings, most likely because of its small natural range. It is designated as near



FIGURE 1. Adult (left) and juvenile (right) Colorado Checkered Whiptail (*Aspidoscelis neotesselatus*). (Photographed by Douglas Eifler).

threatened by the International Union for Conservation of Nature (IUCN 2007), is a species of special concern by Colorado Parks and Wildlife, and the U.S. Army lists it as a species at risk. Its known natural range is located in a relatively small area in southeastern Colorado, within six counties, significantly large parts of which encompass the Fort Carson (FC) Military Installation (Fig. 2) in El Paso, Fremont, and Pueblo counties (55,442 ha) and Piñon Canyon Maneuver Site in Las Animas County (95,504 ha).

The demography of *A. neotesselatus* (sub)populations has not been investigated; how it persists in local abundance within parts of the natural range in southeastern Colorado is intriguing. In particular, uncertainty about the status of *A. neotesselatus* in FC in response to the impact of military readiness activities on their demography and fitness led to the presence study. Our objectives were to provide an understanding of the abundance of *A. neotesselatus* within the different (sub)populations located in FC, how it fares across military training locations, and further estimate baseline demographic information regarding both survival and reproductive output at the northern edge of the range. We specifically estimate an abundance index via a catch-per-unit estimator, weekly survival using Cormack-Jolly-Seber models, body condition, and clutch size, as indicators of stability. Importantly, the study also lays the foundation for future monitoring of *A. neotesselatus* in FC, which will ultimately help in the management of this species, as there is currently no systematic monitoring for it in place at this military installation, or anywhere else to our knowledge.

MATERIALS AND METHODS

Site selection and field activities.—The U.S. Army installation known as FC is located in unincorporated El Paso County, Colorado, near the city of Colorado Springs. The 55,000 ha installation extends southward

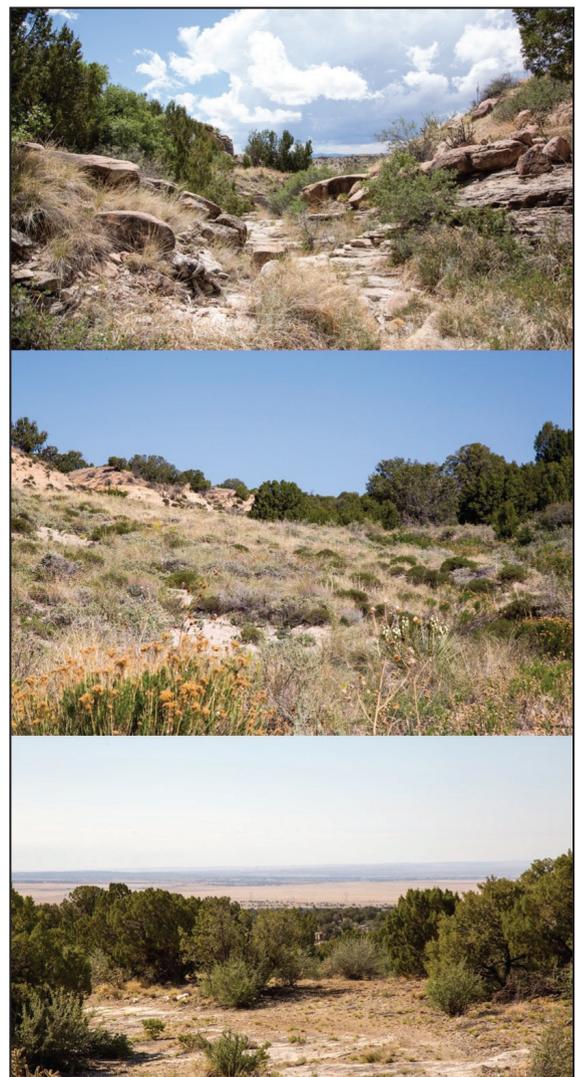


FIGURE 2. Habitats of Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) at Fort Carson, Colorado, USA. (Top) training area (TA) 45, (Middle) TA 48, (Bottom) TA 55. (Photographed by Douglas Eifler).

into Pueblo and Fremont counties. We sampled and surveyed *A. neotesselatus* at the northern edge of its range in FC. Site selection required working around the constraints of scheduled military training activities. We did not observe the first lizard until 28 April 2018, and we had severely limited access to most sites throughout the study. Of the 36 training areas (TA; numbered 20–56) that may provide suitable habitat for *A. neotesselatus* within FC, we were interested in surveying the TAs where recent surveys had indicated *A. neotesselatus* activity (i.e., observations in 2014: TAs 28, 29, 31, 43; observations between 2007 and 2013: TAs 45, 48, 50, and 56). We were provided access to five of those TAs (29, 45, 48, 50 and 55). The number of lizards observed was insufficient to support meaningful demographic and physiological sampling at TA 29 and 50. As a result, intensive sampling was focused on TA 48 and eventually TA 55, while efforts were made to identify additional sites. We attained sufficient sample size to be able to estimate and report indices of abundance and fitness at TA 45, 48, and 55. The area we surveyed covered 0.99 ha for TA 45, 6.12 ha for TA 48, and 4.85 ha for TA 55, respectively, and were similarly exposed to low levels of military training activities (i.e., on-foot navigation and orientation). We considered these sites the relatively least disturbed areas in FC. We did not observe gonochoristic *A. sexlineatus* (Six-lined Racerunner) in syntopy with parthenogenetic *A. neotesselatus* at FC, although *A. sexlineatus* is known to occur there.

Prior to our effort on the ground, we conducted a preliminary survey in 2016 to generally assess presence, catchability, and physiology of *A. neotesselatus* sampled from the two distinct strata: stratum A was comprised of TAs 48, 50, and 52, whereas stratum B was comprised of TAs 28, 29, and 41. Sample sizes reached at the time were very low, thus, to improve the number of captured and recaptured individuals, we increased manpower (field crew of 6–10 individuals) and time spent in the field in 2018 (3 mo) in comparison to the preliminary 2016 study that only took place over two weeks. We surveyed our primary site (TA 48) 22 times, spanning the sampling periods. This was the only site at which we had consistent access across the entire lizard active season (i.e., at emergence, at the time of first clutch,

second clutch, and before dormancy). We used the data collected over those occasions to estimate monthly survival in 2018 and abundance based on an effort index. We also conducted the demographic and physiological analyses from data collected at TAs 45 and 55, where acceptable sample sizes were reached (Table 1). TAs 50, 52, 28, 29, and 41 were not consistently accessible to us in 2018.

The field season ranged from late April 2018 to end of July 2018 and expanded on our 2016 pilot physiology study where we sampled and marked 86 individuals over three locations at FC (91 observations, five of which were recaptures) over a 3-mo period. *Aspidoscelis neotesselatus* was most active between 0800 and 1100; field crews were typically deployed between 0700 and 1200 to conduct both Capture-Mark-Recapture (CMR) and transects surveys. Field crews of 2–3 members were involved in CMR efforts each day: while we conducted transect surveys less frequently. We captured and surveyed lizards on different sites, for any given day, to help ensure that trapping activities did not affect the ability to find lizards when conducting transect surveys. Access to sites, conditional on military activities, dictated that we visited certain sub-populations more frequently than others.

We observed *A. neotesselatus* within habitat with Piñon Pine (*Pinus edulis*), Ponderosa Pine (*Pinus ponderosa*), and mixed oak trees (*Quercus* sp.), as well as the cactus Tree Cholla (*Cylindropuntia imbricata*) and the grass Blue Grama (*Bouteloua gracilis*), which dominated grasslands in TA 45 (Fig. 2). The majority of *A. neotesselatus* we observed in the TA 48 study site were concentrated within the dry creek bed and banks, consisting of sparsely vegetated shrubland, particularly Shadscale (*Atriplex confertifolia*), Four-wing Saltbush (*Atriplex canescens*), James' Seaheath (*Frankenia jamesii*) and Rubber Rabbitbrush (*Chrysothamnus nauseosus*). The secondary vegetation type was One-seeded Juniper (*Juniperus monosperma*) and mixed grassland, located around the periphery of the sample area (Fig. 2). TA 55 was similar in habitat structure to TA 48 and we surveyed this site 16 times (Fig. 2).

We conducted CMR opportunistically within a site based on activity levels in an effort to maximize (re) capture rates. We noosed lizards (Bloomberg and

TABLE 1. Sample sizes of Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) by military training area (TA) at Fort Carson, Colorado, USA; this includes all sightings-captures and resightings by habitat type and training area. The abbreviation cwd = coarse woody debris.

TA	cactus	cwd	grass	juniper	open	open gravel	open rock	open sand	vegetation/shrub	Grand Total
45	4		4	5	1	1	2	2	3	22
48		7	14	53	28	70		22	119	313
55	1	13	9	24	24	13	21	1	66	173
Total	5	20	27	82	53	84	23	25	188	508

Shine 2006), which we successfully tested as part of the 2016 survey. We permanently marked each captured individual by toe-clipping in the field, which has been found to be harmless to *A. neotesselatus* (based on a preliminary physiological survey that took place in 2016; see also Langkilde and Shine 2006). We recorded the date, time of day, body mass (g), and snout-vent length (SVL; mm) for each captured animal. To assess gravidity, clutch size, and follicular/egg volume (informing the reproductive state and potential reproductive output of each marked animal), we checked abdomens of females with a high definition Sonosite Turbo ultrasound unit with an external linear probe (Sonosite Turbo ultrasound, FUJIFILM SonoSite Inc., Bothell, Washington, USA). Once we collected these data, we immediately released lizards at the exact point of capture.

Index of abundance.—We originally intended to use distance sampling to attain estimates of abundance of *A. neotesselatus* from transect surveys (Laake 1993). Distance-sampling methods are attractive in many animal-sampling problems because they do not require that individuals be uniquely marked and recaptured (or resighted) through time. Conventional distance sampling is based on the estimation of a detection function, $g(x)$ in the case of line transects, which decreases with distance (x) and is needed to estimate *A. neotesselatus* detection probability given availability (P_d). Because transects were insufficiently close to allow for good detection, however, and because of the active need to search an entire patch to reach sufficient detection, we settled on an alternative approach borrowed from fisheries surveys: the Catch-Per-Unit Effort (CPUE) estimator, to obtain estimates of abundance for each TA surveyed. Use of CPUE (Leslie and Davis 1939; Laake 1992; Lancia et al. 1996) can be used to estimate absolute abundance of closed populations. This estimation is possible because of the proposed relationship between survey effort and likelihood of an animal being seen in our case, as well as the observed plateau in the likelihood of observing new animals as a delimited area gets surveyed.

On the CPUE plots presented below for each TA, the effort index on the x-axis provides an indication of time spent searching for animals within the surveyed plot. CPU, on the y-axis, represents the number of animals sighted up to a given point in the survey. When the relationship tappers off, one we can assume that maximum abundance for a given plot has been reached. To increase sample size, we combined the different surveys that were conducted at each site to produce CPU curves.

In practice, we systematically walked an entire study site. We marked the boundaries of study areas with flagging or we used natural boundaries, such as ridges

or cliff edges. Observers (two to three teams of three) walked parallel paths through a study area, moving over as a site boundary was reached, and repeating the process until the entire site was surveyed. Researchers maintained a distance of about 10 m separation, in an effort to maximize detection of all active individuals of *A. neotesselatus*. During surveys, we did not capture animals, but noted color codes of marked animals. We also recorded habitat information for each sighting: estimates of open ground, shrub, grass, juniper, cactus, debris.

Body condition index.—We investigated the impact of TA, age, habitat, and relevant interactions on both body mass and body condition separately. Because the relationship between body mass and SVL was curvilinear, we log-transformed both variables to linearize the relationship, then used residuals from the linear relationship as an index of body condition.

Capture-Mark-Recapture survival estimation.—We estimated biweekly (15-d window) survival for the three TAs we sampled at FC. We used Cormack-Jolly-Seber (CJS; Lebreton et al. 1992) CMR models developed in R using the RMark package (Laake et al. 2013) to estimate apparent survival (ϕ) and recapture probability (p) for each TA. We then used QAICc to score the top model(s) in the considered model set (Burnham and Anderson 2004), where the lower the score, the better the model fit to the process that gave rise to the data. Because sample size was limited, estimates of apparent survival were not attainable at TA 45. For TA 48 and 55, we excluded models where estimates did not converge (i.e., models that are over-parameterized given data availability). We consider four models for each TA: $p(.) \phi(.) / p(t) \phi(.) / p(.) \phi(t) / p(t) \phi(t)$, where (t) is time-variation between capture occasions, and (.) stands for no change over time (i.e., survival or detection probabilities across time intervals are set to be equal to one another).

Clutch size and volume.—For each adult of *A. neotesselatus* captured, we collected a maximum of four samples (at emergence, 1st clutch, 2nd clutch, post reproduction) because recapture probabilities were low and only one sample was obtained from some captured lizards. Using both manual palpitation of the abdomen to assess the number and firmness of follicles/eggs as well as ultrasound, we assessed female reproductive state and classified reproductive output as zero, one follicle, two follicles, three follicles, one egg, two eggs, or three eggs. We built a Two-way Contingency Table and used Chi-square to test the null hypothesis that there is no significant difference between the expected (under the chi-square distribution) and the observed frequencies of clutch size outcomes (i.e., zero, one to

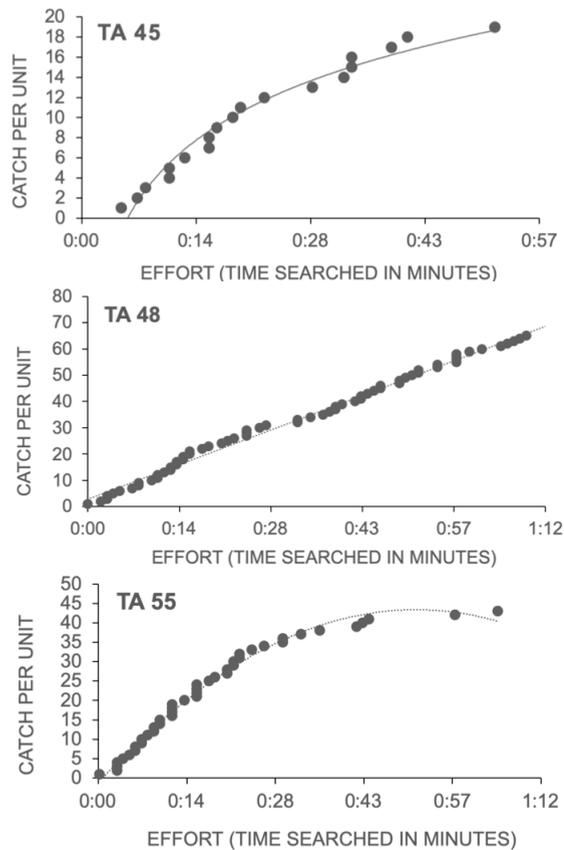


FIGURE 3. Catch curves of individual Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) per unit effort (CPUE; in minutes) for each training area (TA) for surveys performed in 2018 at Fort Carson, Colorado, USA. (Top) CPUE at TA 45, Fort Carson, based on two plot surveys. (Middle) CPUE at TA 48, Fort Carson, based on two plot surveys. (Bottom) CPUE at TA 55, Fort Carson, based on three plot surveys.

three follicles, one to three eggs, with eggs and follicles treated as separate entities) across TAs (TA 45, 48, and 55). We conducted statistical analyses using R version 3.2.3 (R Core Team 2015) with the exception of the CMR analysis, which we performed in program MARK, version 8.2 ($\alpha = 0.05$ for all tests).

RESULTS

Of the three TAs sampled over the spring and summer, TA 45 was the most productive site, with the highest densities of *A. neotesselatus* and the highest frequency of reproductive females. We captured the most lizards in TA 48, and lizard across all TAs were mostly found in shrub habitat, open gravel, and juniper (Table 1). The relationship between CPU and Effort was linear for TAs 45 and 48, as opposed to a bounded relationship for TA55. Based on these CPUE curves (Fig. 3), we estimate minimum densities of 19.2 lizards/

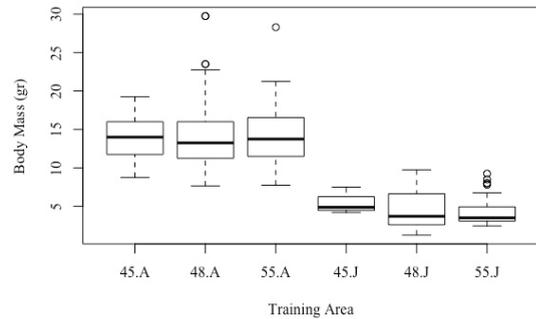


FIGURE 4. Body mass differences across age classes (J = juveniles, A = adults) of Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) and training areas (TA) at Fort Carson, Colorado, USA.

ha for TA 45, 10.62/ha for TA 48, and 8.68/ha for TA 55.

Body mass significantly varied by age class, with juveniles weighting less on average than adults (mean juveniles = 4.57 g; mean adults = 13.88 g; $t = 45.55$, $df = 598.98$, $P < 0.001$; Fig. 4). Juvenile body mass did not significantly differ among TAs ($F_{2,213} = 0.331$, $P = 0.719$; Fig. 4), and similarly for adult body mass ($F_{2,577} = 1.430$, $P = 0.240$; Fig. 4). There also was no significant interaction between age class and TA ($F_{2,790} = 0.720$, $P = 0.487$). Body condition also did not differ significantly by age class (mean juveniles = -0.013 ; mean adults = 0.005 ; $t = 1.72$, $df = 352.79$, $P = 0.086$) or among TAs ($F_{2,793} = 2.650$, $P = 0.071$), nor was there a significant interaction ($F_{2,790} = 0.136$, $df = 2$, $P = 0.873$). Body condition of lizards did, however, differ significantly between two general habitat categories: open (mean open habitat = -0.013) versus cover (mean under cover = 0.010 ; $t = 2.45$, $df = 753.82$, $P = 0.014$; Fig. 5).

At TA 48, we captured 311 animals, 103 of which were recaptures. Although the model selection process indicated that the $\phi(\cdot) p(t)$ model outperformed other models, only the $\phi(\cdot) p(\cdot)$ model provided reliable estimates of ϕ and p (Table 2). Estimates indicate that apparent survival for a two-week period was 0.878 (Table 3). TA 48 monthly apparent survival for the species was $0.878^2 = 0.771$. Detection probability was estimated with good precision ($p = 0.144$; 95% CI = 0.092–0.219) and was rather low despite our best efforts. At TA 55, we captured 174 animals, 57 of which were recaptures. The model selection process indicated that the $\phi(\cdot) p(\cdot)$ model slightly outperformed more complex models, likely because of sample size limitations. Estimates below indicate that apparent survival for a two-week period was 0.799 with a monthly apparent survival of $0.799^2 = 0.638$. Unlike survival probability (95% CI = 0.311–0.972), detection probability was estimated with good precision ($p = 0.241$; 95% CI = 0.165–0.339).

The observed clutch size distribution differed significantly from the expected distribution ($\chi^2 = 30.87$, $df = 12$, $P = 0.002$). This departure was found to be

TABLE 2. Model selection results for Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) for training area (TA) 48 and 55: estimation of apparent survival Φ corrected for imperfect detection p using the Cormack Jolly Seber open population model in program MARK. Models are compared based on QAIC, and include time variation in Φ , no variation in Φ , time variation in p , no variation in p , and respective combinations. The abbreviation NP = the number of parameters.

Model	QAIC	NP
TA 48		
$\phi(\cdot)p(\cdot)$	406.3192	2
$\phi(\cdot)p(t)$	399.8437	5
$\phi(t)p(\cdot)$	405.2701	3
$\phi(t)p(t)$	402.5361	7
TA 55		
$\Phi(\cdot)p(\cdot)$	271.9850	2
$\Phi(t)p(\cdot)$	270.2993	3
$\Phi(t)p(t)$	269.8843	4
$\Phi(\cdot)p(t)$	269.9113	3

significant between TA 45 and TA 48 ($\chi^2 = 16.94$, $df = 6$, $P = 0.009$), not significant between TA 48 and 55 ($\chi^2 = 10.49$, $df = 6$, $P = 0.105$), and inconclusive between TA 45 and TA 55 for lack of data. Females at TA 48 were significantly more productive than at the other two sites, although fewer females were reproductive (Fig. 6). We recorded the most observations of clutch size at TA48, followed by TA 55, then TA 45 (Fig. 6).

DISCUSSION

Reptiles play a key part in the proper functioning of ecosystems via their role in food webs where they serve as herbivores, insectivores, predators, and prey (Schenider et al. 2001). A large portion of reptile diversity worldwide is currently in peril (Dirzo and Raven 2003), and in North America alone, 12% of snakes and lizards are in threat of extinction (NatureServe.

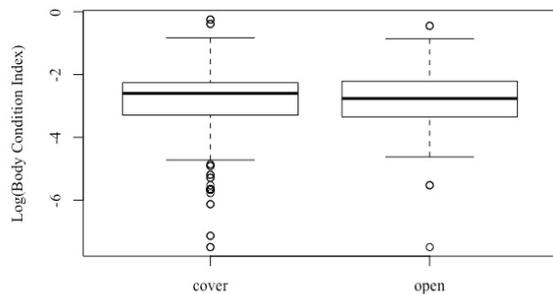


FIGURE 5. Significant body condition differences (log-scale) of Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) between open (open sand, gravel, rock, and grass) and closed habitat types (cactus, coarse woody debris, shrub, and juniper) at Fort Carson, Colorado, USA.

TABLE 3. Parameter estimates from the most parsimonious model selected from $\Phi(\cdot)p(\cdot)$ is the only model that provided reliable estimates of Φ and p . Mean parameter estimates are presented along with standard error and 95% confidence intervals (CI) for training area (TA) 48 and 55.

	Parameter Estimates	Standard Error	Lower bound (95% CI)	Upper bound (95% CI)
TA 48				
Φ	0.8775702	0.0827428	0.6130556	0.9700862
p	0.1440390	0.0319712	0.0919217	0.2185926
TA 55				
Φ	0.7989373	0.1780392	0.3115951	0.9721318
p	0.2412128	0.0446508	0.1646275	0.3389692

2007. New assessment of North American reptiles finds rare good news. NatureServe, Arlington, Virginia, USA. Available from www.natureserve.org [Accessed 18 June 2019]. Reptiles are susceptible to many anthropogenic threats, such as habitat fragmentation, urbanization, invasive species introductions, pollution, and global climate change (Gibbons et al. 2000), but many species are poorly studied (Urbina-Cardona 2008). Addressing the issue of data insufficiency will be key in preventing future declines in reptile species that may be on the verge of collapse.

Aspidoscelis neotesselatus is a small triploid parthenogenetic reptile, which is endemic to parts of Colorado (Walker et al. 1997a; Taylor et al. 2015a), though it has also become established in Washington state (Weaver et al. 2011). Our overarching goal was to conduct the most thorough demographic monitoring of the species to date within the part of FC in El Paso County, Colorado. This not only encompassed a significant portion of the range of the species, it is also the part of the range within which it is least understood. We were limited in our ability to survey the site based

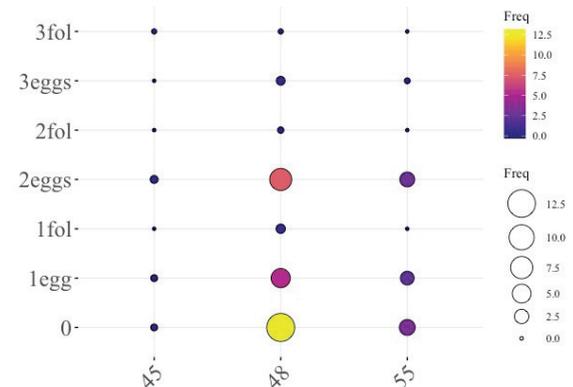


FIGURE 6. Relative frequencies of clutch size output (zero, one, two, or three follicles; one, two, or three eggs) for Colorado Checkered Whiptails (*Aspidoscelis neotesselatus*) across training areas (TA) 45, 48, and 55 at Fort Carson, Colorado, USA.

on day-to-day military training activities, but we were able to obtain large sample sizes in three training locations that were similarly low in disturbance levels. Within each TA, we located lizards in their preferred habitat, which included arroyos (steep edge slopes and associated rocky bottomlands), juniper woodland, and cacti.

Minimum lizard densities of 19.2/ha in TA 45 and 8.68/ha in TA 55 are likely reliable given the fact that an asymptote in the CPUE was almost reached at TA 45, and most certainly reached in TA 55. TA 48 and 55 provide good study locations in that they equated to suitable habitat as reported for neighboring Pueblo County (Susan Spackman Panjabi et al., unpubl. report). We caught and recaptured most animals at TA 48, which may simply have to do with the size of this particular training area, quite comparable in size to TA 55, but six times larger than TA 45. We were also able to achieve reasonable sample sizes in TA 45 and TA55, but plan to increase sample size further in 2019 to attain more precise estimates of density.

Although we did observe significant differences in body mass across TAs 48 and 55 within age classes, these differences disappeared once estimates were corrected using the body condition index. Body condition did differ significantly by age class and was less in juveniles than adults but was not significantly different across TAs. Although body condition was slightly higher in TA55, apparent monthly survival was lower at TA 55 than at TA 48 (0.638 versus 0.77) and very low overall considering these are monthly estimates; however, the uncertainty around those estimates was very large, and additional years of CMR data collection will help refine these estimates, and better inform *A. neotesselatus* conservation efforts. In the whiptail lizard *Cnemidophorus* cf. *ocellifer*, average female apparent monthly survival estimates ranged from 0.50 to 0.71 (Guimarães et al. 2017) and were similar to the magnitude observed across the two TAs surveyed.

Across both TA 48 and TA 55, detection probability was low overall, but slightly higher in TA 55 than in TA 48 (0.24 versus 0.14). Until recently, return rates were used as a proxy for survival rates, which leads to a two-fold problem: we could only find one study that reported apparent survival rates for the genera *Aspidoscelis* and return rates confound both the probability of survival and the probability of detecting an animal (Lebreton et al. 1992) because individuals are hard to find in the wild, survival tends to get underestimated (Clobert 1995). CMR models allow for testing biological processes while accounting for the imperfect detection of animals in the wild and is the only reliable tool that should be used to estimate apparent survival conditional on imperfect detection (Lebreton et al. 1992).

Clutch size differences were also observed across training areas. The results further suggest that TA 48

supported the largest frequency of reproductive females that are successful in producing anywhere from one to three eggs. Follicle production was more balanced across TAs, with TA 48 holding a slight advantage; however, most observations were made earlier in the season, prior to the peak in reproductive activity. Another field season will help determine what we have missed by intensifying reproductive sampling during peak reproductive activity.

Overall, our results suggest that TA48 supported a large fraction of reproductive females that were successful in producing eggs and suggest that accessible habitat at Fort Carson supported arrays of *A. neotesselatus* that were reproductively active, survived at low rates (although there is no comparable data available in related whiptail species), were available for capture, but were only recaptured with very low probability despite extensive sampling efforts on the ground. Coarse-scale (i.e., data poor) distribution models developed by the Fort Carson Conservation Branch (Erin Parks and Bryan Kluever, unpubl. report) reveal that habitat available for *A. neotesselatus* encompasses nearly half of FC lands available to training. This means that the proper monitoring and management of the species on FC will be essential in maintain existing populations in years and decades to come. Our recommendation would be to keep current monitoring plans in place, build up the current sampling scheme to help boost sample size and improve estimate precision, construct population viability models once estimates of recruitment become available, and conduct a larger scale occupancy survey as additional TAs become available for survey to assess the extent of the distribution of *A. neotesselatus* on FC.

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LITERATURE CITED

- Baker H.G. 1974. The evolution of weeds. Annual Review of Ecological Systematics 5:1–24.
Bloomberg S., and R. Shine. 2006. Reptiles. Pp. 297–306 *In* Ecological Census Techniques. Sutherland, J. (Ed.). Cambridge University Press, New York, New York, USA.

- Burnham K.P., and D.R. Anderson. 2004. Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304.
- Clobert J. 1995. Capture-recapture and evolutionary ecology: a difficult wedding? *Journal of Applied Statistics* 22:989–1008.
- Dirzo R., and P.H. Raven. 2003. Global state of biodiversity and loss. *Annual Review of Environmental Resources* 28:137–167.
- Gibbons J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653–666.
- Guimarães M., R. Munguía-Steyer, P.F. Doherty, Jr., and R.J. Sawaya. 2017. No survival costs for sexually selected traits in a polygynous non-territorial lizard. *Biological Journal of the Linnean Society* 122:614–626.
- International Union for Conservation of Nature (IUCN). 2007. IUCN Red List of Threatened Species. www.iucnredlist.org.
- Laake J.L. 1992. Catch-per-unit-effort models: an application to an elk population in Colorado. Pp. 44–55 *In* *Wildlife 2001: Populations*. McCullough, D.R., and R.H. Barrett (Eds.). Springer, Dordrecht, The Netherlands.
- Laake J.L., S.T. Buckland, D.R. Anderson, and K.P. Burnham. 1993. DISTANCE user’s guide. Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, Colorado, USA. 72 p.
- Laake J.L., D.S. Johnson, and P.B. Conn. 2013. Marked: an R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture–recapture data. *Methods in Ecology and Evolution* 4:885–890.
- Lancia R.A., C.E. Braun, M.W. Collopy, R.D. Dueser, J.G. Kie, C.J. Martinka, D. Nichols, T.D. Nudds, W.R. Porath, and N.G. Tilghman. 1996. ARM! For the future: adaptive resource management in the wildlife profession. *Wildlife Society Bulletin* 24:436–442.
- Langkilde T., and R. Shine. 2006. How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. *Journal of Experimental Biology* 209:1035–1043.
- Lebreton J.D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Leslie P.H., and D.H.S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. *Journal of Animal Ecology* 8:94–113.
- Parker, E.D., and R.K. Selander. 1976. The organization of genetic diversity in the parthenogenetic lizard *Cnemidophorus tesselatus*. *Genetics* 84:791–805.
- Schneider R.L., M.E. Krasny, and S.J. Morreale. 2001. Hands-on herpetology: exploring ecology and conservation. National Science Teachers Association Press, Arlington, Virginia, USA. 145 p.
- Taylor, H.L., B.A. Droll, and J.M. Walker. 2006a. Proximate causes of a phylogenetic constraint on clutch size in parthenogenetic *Aspidoscelis neotesselata* (Squamata: Teiidae) and range expansion opportunities provided by hybridity. *Journal of Herpetology* 40:294–304.
- Taylor, H.L., L.J. Livo, D.J. Martin, W.R. Maynard, A. Estep, R. Clawges, D. Roth, J. Kellner, and T. Jackson. 2015a. New northern distribution records for pattern classes A, B, and D of *Aspidoscelis neotesselata* (Colorado Checkered Whiptail) in Colorado, and biogeographic sources of northern colonists. *Herpetological Review* 46:312–319.
- Taylor, H.L., R.J. Rondeau, and J. Sovell. 2006b. Alternative ontogenetic pathways to color Pattern Class B in a newly discovered population of parthenogenetic *Aspidoscelis neotesselata* (Squamata: Teiidae). *Herpetological Review* 37:40–44.
- Taylor, H.L., J.M. Walker, C.J. Cole, and H.C. Dessauer. 2015b. Morphological divergence and genetic variation in the triploid parthenogenetic teiid lizard, *Aspidoscelis neotesselata*. *Journal of Herpetology* 49:491–501.
- Taylor, H.L., A.J. Wilmes, L.K. Garey, C.E. Montgomery, L.J. Livo, and J.M. Walker. 2016. Rare color-pattern misfits in indigenous arrays of parthenogenetic *Aspidoscelis neotesselata* (Colorado Checkered Whiptail). *Herpetological Review* 47:561–568.
- Urbina-Cardona, J.N. 2008. Conservation of Neotropical herpetofauna: research trends and challenges. *Tropical Conservation Science* 1:359–375.
- Walker, J.M., J.E. Cordes, and H.L. Taylor. 1997a. Parthenogenetic *Cnemidophorus tesselatus* complex (Sauria: Teiidae): a neotype for *C. tesselatus* (Say, 1823), redescription of the taxon, and description of a new triploid parthenogenetic species. *Herpetologica* 53:233–259.
- Walker, J.M., H. L. Taylor, G. J. Manning, J.E. Cordes, C.E. Montgomery, L.J. Livo, S. Keefer, and C. Loeffler. 2012. Michelle’s lizard: identity, relationships, and ecological status of an array of parthenogenetic lizards (genus *Aspidoscelis*: Squamata: Teiidae) in Colorado, USA. *Herpetological Conservation and Biology* 7:227–248.
- Weaver, R.E., A.P. O’Connor, J.L. Wallace, J.M. King, and J.M. Walker. 2011. Discovery of the parthenogenetic Colorado Checkered Whiptail, *Aspidoscelis neotesselata* (Squamata: Teiidae), in Washington state. *Northwestern Naturalist* 92:233–236.
- Wright, J.W., and C.H. Lowe. 1968. Weeds, polyploids, parthenogenesis, and the geographical and ecological distribution of all-female species of *Cnemidophorus*. *Copeia* 1968:128–138.

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