

Evaluating the Thermal Effects of Translocation in a Large-Bodied Pitviper

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ABSTRACT

Acute stressors can be costly, often requiring alteration of normal physiological processes to mitigate their effects. Animal translocation may be a very stressful event and result in a reduced ability to maintain homeostasis. The impacts of translocation on the thermal ecology of ectothermic vertebrates, which may rely on preferred habitats for thermoregulation, are currently unknown. In this study, 22 adult male Northern Pacific rattlesnakes (*Crotalus oreganus oreganus*) were implanted with automated temperature loggers and radio-tracked. Snakes were assigned to one of three treatments: translocation, handling control, and undisturbed control. Short-distance translocation (SDT) and handling treatments were applied weekly for 6 weeks. Hourly body temperature (T_b) was recorded during the course of the study. Mean T_b was impacted in a time-dependent fashion, where translocated snakes had lower mean T_b than handled controls during the first week of the study only, especially the first 24 hr after translocation. Separating the dataset into day and night revealed that this effect was localized to T_b variation during the day only. Variance in temperature was not impacted by translocation or handling. Snake body mass and time of year were the major factors influencing the thermal profiles of these rattlesnakes. Thermal ecology in male rattlesnakes is resilient to SDT, suggesting that they quickly resume normal behaviors following repeated bouts of acute capture stress and disturbance of their spatial ecology. This study provides support for SDT as a safe measure for mitigating human–snake interactions and facilitating conservation practices regarding male snakes, which are the most frequently encountered sex. *J. Exp. Zool.* 9999A: XX–XX, 2014. © 2014 Wiley Periodicals, Inc.

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Characterizing an organism's physiological response to acute stressors is a powerful means of understanding the adaptations used in averting homeostatic disturbance, pinpointing threshold levels of allostatic load for different types of stressors, and predicting downstream effects on physiological performance and life-history traits that might be incurred due to anthropogenically-induced stressors. Techniques used in research, conservation, and management (capture, confinement, translocation, radiotelemetry, etc.) could be highly influential forms of human disturbance on local populations. While direct physiological stress associated with capture and confinement has often been measured via acute

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hormonal stress responses (Dunlap and Wingfield, '95; Dickens et al., 2010), we remain relatively uninformed about how individual organisms respond physiologically to management practices across longer timeframes (i.e., week to months), during repeated bouts of stress, and in physiological traits aside from adrenocortical secretion.

Translocation is a commonly used conservation strategy and management practice for mitigating the negative impacts of human-wildlife interactions. The translocation of problematic or nuisance animals has become a popular, non-lethal management method (reviewed in Fischer and Lindenmayer, 2000). The goal of a translocation is to relocate the nuisance animal to another location of suitable habitat away from humans, thereby removing it from potential negative interactions with people. Additionally, translocation has been extensively investigated as a potential tool for conservation biology (Dodd and Seigel, '91; Seddon et al., 2007; Besson and Cree, 2011). This method can be used to augment a population to increase its genetic viability (Madsen et al., '99) or to increase and/or expand a species' current range (McLachlan et al., 2007; Besson and Cree, 2011). While some studies have documented the impacts of translocation on movement and mortality (Butler et al., 2005; Brown et al., 2009; Roe et al., 2010), few have looked at the potential physiological impacts associated with translocation.

Ectotherms rely heavily on behavioral thermoregulation and the use of sites containing specific thermal microhabitats (Row and Blouin-Demers, 2006; Gardner-Santana and Beaupre, 2009). Movement away from preferred thermal microhabitats during translocation represents a risk unique to ectothermic vertebrates, as temperature and its variation have proximate impacts on growth, performance, stress physiology, and reproduction (Kaufmann and Bennett, '89; Cree et al., 2003; Aidam et al., 2013). These physiological consequences of translocation could conceivably lead to reduced ability to avoid predators and less time for foraging, eventually leading to a decrease in the health of ectotherms subjected to translocation, especially if the same animals must be repeatedly translocated because they move back. The rattlesnake translocation program at Arizona's Sonoran Desert Museum had translocated the same male Western Diamond-backed Rattlesnake (*Crotalus atrox*) 49 times as of June, 2011 (S. Poulin, pers. comm.). Because translocation is such a commonly used mechanism in conservation and management (reviewed in Fischer and Lindenmayer, 2000), additional studies are needed to address the potential physiological impacts of translocation on wildlife.

Rattlesnakes are a taxonomic group of particular interest in regard to translocation, as rattlesnakes are often considered a nuisance or potential threat to humans (Nowak et al., 2002), and several species are of conservation concern (Brown, '93; Gibbs et al., '97; Waldron et al., 2008). Short-distance translocation (SDT), defined as the transport of an animal to a location near or within its home range (Hardy et al., 2001), has no known negative

impacts on translocated rattlesnakes (Brown et al., 2009; Holding et al., in press). In contrast, long-distance translocation (LDT) employs the relocation of a snake outside of its home range (Hardy et al., 2001), often many miles away. Though LDT has been shown to prevent the return of snakes to the capture area, it is often not recommended due to the potential increase in mortality of translocated individuals (Reinert and Rupert, '99). While the impacts of SDT on rattlesnake movement (Brown et al., 2009), stress physiology (Holding et al., in press), neuroanatomy (Holding et al., 2012), and mortality (Brown et al., 2009) have been investigated, effects related to the ecologically important parameter of temperature remain unknown. Here we tested the hypothesis that repeated SDT and handling represent thermal stressors to rattlesnakes by analyzing temperature data collected during a field experiment on the Northern Pacific Rattlesnake (*Crotalus oreganus oreganus*). If SDT represents a chronic thermal stressor to rattlesnakes, then mean body temperature (T_b) and variance in T_b in *C. o. oreganus* are expected to differ between translocated and non-translocated snakes.

MATERIALS AND METHODS

Capture and Surgical Implantation

The study took place from March to June 2010 at the Chimineas Ranch unit (35°09' N, 119°57' W; elevation ~790 m) of the Carrizo Plain Ecological Reserve in San Luis Obispo County, CA. Twenty-two large adult male (>80 cm snout-to-vent length) *C. o. oreganus* were captured by visual search in March and early April. The study area consisted primarily of rolling, grassy hills, scattered rocky outcrops, and blue oaks (*Quercus douglasii*), with heavy grazing of horses and cattle.

Capture and implantation of radio-transmitters are described in Holding et al. (2012, in press). Briefly, snakes were anesthetized through inhalation of isoflurane gas and implanted intracoelomically with radio-transmitters (SI-2, Holohil Systems Ltd., Carp, Ont., Canada).

During surgery, a Thermochron iButton (Maxim Integrated, San Jose, CA) programmed to record T_b every hour and coated twice with heavy-duty rubber coating (Plasti Dip[®], PDI, Inc., Circle Pines, MN) and sterilized overnight in benzalkonium chloride (Benz-all[®], Xttrium Laboratories, Chicago, IL) was implanted into the body cavity alongside the radio-transmitter and secured with suture to a rib to prevent movement. Semi-continuous sampling such as this provides far superior thermal data on free-ranging animals than point-sampling, for example, with temperature-sensitive radiotelemetry (Taylor et al., 2004). Following 1–3 days of recovery in the lab, snakes were returned to the field (Row and Blouin-Demers, 2006).

Experimental Translocation

We randomly assigned snakes to one of three experimental groups: translocated ($n = 8$), handled but not translocated ($n = 8$),

or undisturbed control ($n=6$). One handled snake required a second surgery due to radio-transmitter failure and it has been excluded from this study. The translocated snakes received weekly (every 7–8 days) 225 m translocations in the form of a randomly selected (see Holding et al., 2012, in press), straight-line displacement while being carried in a plastic bucket. We chose the 225 m distance as a short-distance translocation because snakes were placed at or near the boundaries of their current home ranges (based on data on home range size of snakes at the same study site; Putman et al., 2013). The handled snakes were also captured weekly, but were transported in a white plastic bucket over a straight-line distance of 112.5 m away from and 112.5 m back to the site of capture and released, such that they were handled exactly the same way as the translocated group but were not translocated. Translocation and handling treatments were applied on each Friday or Saturday of the study period by capturing snakes with tongs, as all snakes could be visited within 1 day, and any snakes that were below ground were revisited the following day to apply treatment. These snakes spend the majority of the day on the surface or in the mouths of large burrows, facilitating frequent capture without the need to disturb habitat by digging, and treatment was always accomplished by the second attempt during each week. The control snakes were only radio-tracked to record movements, thus we only handled these animals at the beginning and end of the study period. We measured movement distance using a handheld GPS unit (Garmin Legend, Garmin) and placed translocated snakes in the nearest suitable cover. Snakes were tracked in different orders each day to avoid confounding effects of time of day on snakes' responses to experimental treatment. Tracking, handling, and translocation of snakes were initiated on April 30, 2010, allowing at least 10 days of field recovery from surgeries. Application of treatments occurred approximately weekly until June 5, 2010, resulting in six total translocations or handlings per translocated and handled snake.

Data Analysis

We evaluated potential impacts of SDT on the thermal ecology of *C. o. oregonus* using the repeated-measures general linear model (GLM) function in SPSS (IMB Corporation) to model weekly mean T_b and weekly variance in T_b . We calculated mean T_b and variance in T_b within each week (Sunday–Saturday) using each hourly temperature reading (168 total readings per week per snake) collected from 00:01 on Sunday to 23:01 on the following Saturday as a data point to calculate that week's mean or variance. This design allowed us to include week as a within subjects factor to control for seasonal impacts as spring progressed into summer, while day-to-day variation was averaged across the weekly estimate. Treatment group (control, handled, or translocated) was included as a between-subjects factor. During the initial stages of data analysis, body mass was included as a covariate in each model due to its predicted impacts on temperature variation due to thermal inertia. Mass was subsequently removed from our model

of weekly mean T_b due to its non-significance ($P=0.82$) and low partial R^2 value (0.04) as a means to conserve degrees of freedom. Thus, we present a model of weekly mean T_b that included main effects of week and treatment group and an interaction between week and treatment group. Our model of weekly variance in T_b included main effects of week, treatment group, and mass, and two-way interactions between week and the between-subjects predictors treatment group and mass. All variables met the assumptions of normality and homogeneity of variances. Maunchly's test of sphericity was used to evaluate the sphericity assumption of the repeated-measures GLM. The weekly mean T_b data were not spherical, so the Greenhouse-Geisser adjustment was applied to our F -statistics for that model. We downloaded daily maximum air temperatures from the National Oceanic and Atmospheric Administration's (NOAA) National Climatic Data Center collected by the Carrizo Plain weather station 18.8 km southeast of the study site. Weekly mean air temperatures were overlaid on graphs of mean body temperature for visual comparison with snake body temperature data.

Diurnal T_b in ectotherms is largely affected by behavioral thermoregulation, while overnight lows in ambient temperature play a larger role in nocturnal patterns of T_b variation (Angilletta et al., 2002). To account for this, we split the data used for the overall mean and variance analyses into two datasets, one containing only measurements taken during daylight hours, the other only measurements taken during the night. We used sunrise and sunset times for the study period (www.timeanddate.com) to categorize data. We also explored diurnal and nocturnal variation in T_b by analyzing weekly averages for maximum and minimum temperatures. To assess whether translocation impacted daytime and nighttime mean T_b and minimum and maximum T_b in these rattlesnakes, analyses were conducted in a manner identical to those of the full dataset described above.

To examine potential acute impacts of translocation, we extracted mean T_b and variance in T_b for the 24 hr following each application of experimental translocation or handling. For control snakes, we used the 24 hr that followed our visit to the snake on each Friday, during which time snakes in the other experimental groups were translocated or handled. Both mean T_b on day of treatment and variance in T_b on day of treatment were analyzed with a linear mixed effects model in SPSS so that individual variation among snakes could be modeled as a random effect. Our models for both mean and variance in T_b included a repeated effect of week (six levels, one for each week) and a snake ID as a random effect. A first-order autoregressive covariance structure was selected for the repeated effect, while a scaled identity covariance structure was chosen for the random effect. Treatment group was included as a fixed effect, while mass and the time of day that each snake was visited were included as covariates. Additionally, a treatment group by week interaction was included. An alpha of 0.05 was used to evaluate significance of all test statistics, and significant model effects were explored

further using Dunn–Sidak adjusted post-hoc comparisons. In order to better understand the short-term impacts of translocation, 4-day hourly temperature profiles for representative snakes in each treatment group were created and qualitatively inspected.

RESULTS

Increasing ambient temperature over the course of the study was the predominant factor impacting weekly mean T_b , as the main effect of the within-subjects factor week explained an ever-increasing mean T_b ($F_{5,90} = 121.5$, $P < 0.001$, partial $R^2 = 0.87$) as ambient temperatures increased from April to June. There was no main effect of SDT on weekly mean T_b in these snakes ($F_{2,18} = 0.33$, $P = 0.33$; Fig. 1), but the week by treatment group interaction term was significant ($F_{10,90} = 2.13$, $P = 0.030$, partial $R^2 = 0.19$). Post-hoc analyses revealed that the interaction was due to an ephemerally lower mean T_b in translocated snakes during the first week only. Week one mean T_b was significantly lower in translocated snakes (Mean \pm 95% CI = $20.3 \pm 0.96^\circ\text{C}$) than handled snakes ($21.6 \pm 0.62^\circ\text{C}$; $P = 0.032$) but not control snakes (21.2 ± 0.54 ; $P = 0.143$). Post-hoc comparisons did not detect differences in mean T_b among groups for any other weeks of the study ($P > 0.2$).

Weekly variance in T_b was also unaffected by translocation, as there was no main effect of treatment group on weekly variance in T_b ($F_{2,17} = 0.58$, $P = 0.571$; Fig. 2), nor did treatment group interact significantly with the within-subjects factor of week ($F_{7,3,85} = 1.56$, $P = 0.163$). Significant main effects of week ($F_{3,6,85} = 2.75$, $P = 0.021$, partial $R^2 = 0.16$) and the covariate body mass ($F_{1,17} = 8.4$, $P = 0.010$, partial $R^2 = 0.33$) accounted for a moderate amount of the variance in T_b . Body temperature became less variable overall as the study progressed (Fig. 2). The

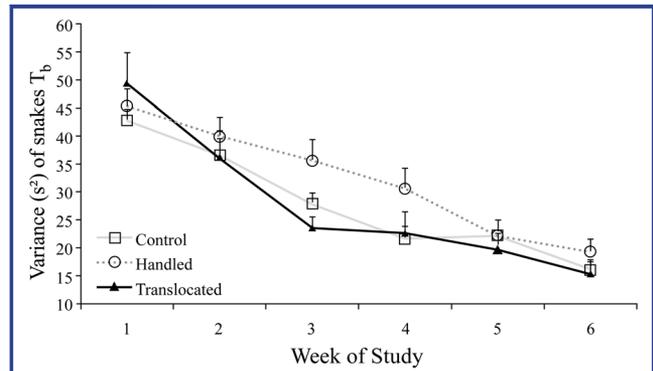


Figure 2. Weekly variance (s^2) in body temperature (Mean \pm 1 SEM) of translocated, handled, and undisturbed control *Crotalus oreganus oreganus* over the 6-week study.

week by mass interaction was not significant in our model of weekly variance in T_b ($F_{5,85} = 1.1$, $P = 0.364$). A post-hoc linear regression of body mass and variance in T_b across the entire study indicated a negative relationship ($\beta = -0.013$, $P = 0.003$, $R^2 = 0.32$).

Splitting the dataset into daytime and nighttime temperatures provides insight into the time-dependent impacts of treatment on mean T_b . Specifically, daytime mean T_b was significantly impacted by a main effect of the repeated effect of week ($F_{5,90} = 109.6$, $P < 0.001$, partial $R^2 = 0.86$), while there was not a significant main effect of treatment group ($F_{2,18} = 1.13$, $P = 0.342$). The week by treatment group interaction was significant in this daytime dataset ($F_{10,90} = 2.01$, $P = 0.042$, partial $R^2 = 0.18$), with translocated snakes having lower week 1 daytime mean T_b (Fig. 3). Just

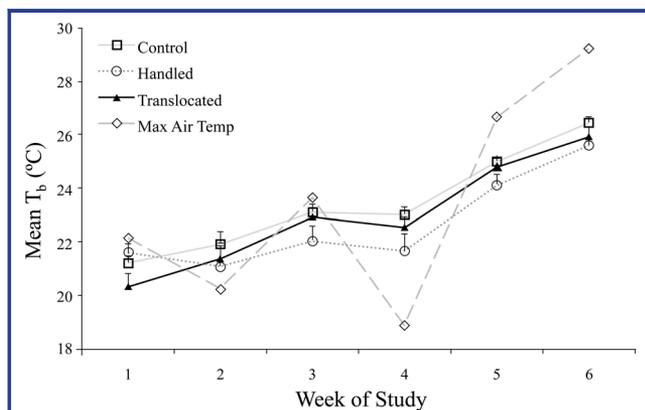


Figure 1. Weekly mean body temperatures ($^\circ\text{C}$, ± 1 SEM) of translocated, handled, and undisturbed control *Crotalus oreganus oreganus* over the 6-week study. Mean weekly maximum air temperatures from a nearby weather station are included for reference and demonstration of behavioral thermoregulation.

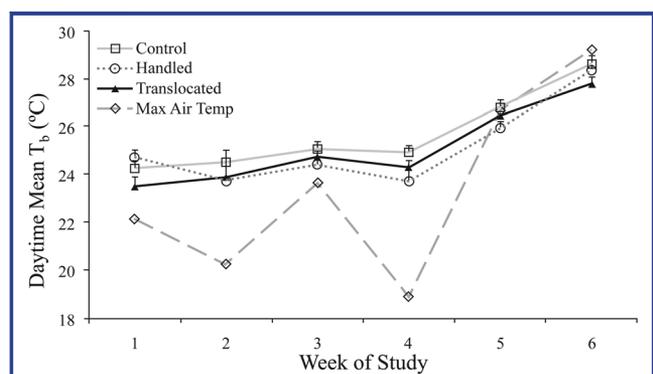


Figure 3. Weekly mean body temperatures ($^\circ\text{C}$, ± 1 SEM) during the daytime hours only for translocated, handled, and undisturbed control *Crotalus oreganus oreganus* over the 6-week study. Mean weekly maximum air temperatures from a nearby weather station are included for reference and demonstration of behavioral thermoregulation.

as in the daytime, nighttime mean T_b was significantly impacted by the main effect of week ($F_{5,90} = 144.3$, $P < 0.001$, partial $R^2 = 0.89$) and there was no impact of treatment group ($F_{2,18} = 1.17$, $P = 0.33$). Notably, however, the week by treatment group interaction was not a significant variable in the nighttime dataset ($F_{10,90} = 1.25$, $P = 0.277$). Separate analyses of the daytime and nighttime variance in T_b were perfectly congruent with analysis using the full data set, and are not presented. Daily minimum and maximum temperatures were unaffected by any model parameters (Table S1).

Modeling mean T_b during the 24 hr immediately after application of translocated, handled, or control treatments revealed congruence with previous analyses of the full weekly temperature dataset, as week had a significant main effect on mean T_b ($F_{5,10} = 50.4$, $P < 0.001$), and there was a significant interaction between treatment group and week ($F_{10,18} = 3.6$, $P = 0.009$). There were no significant main effects of treatment group ($F_{2,16} = 2.51$, $P = 0.11$), mass ($F_{1,14} = 1.12$, $P = 0.31$), or time of day that treatment was applied ($F_{1,83} = 0.04$, $P = 0.83$). Post-hoc inspection of estimated mean T_b for each treatment group generated by our linear mixed model indicated that, like in the full weekly dataset, this interaction was fueled by lower mean T_b during only the first application of treatments (e.g., week 1) in translocated snakes (Mean \pm 95% C.I. = $16.03 \pm 1.5^\circ\text{C}$) compared to handled snakes ($19.29 \pm 1.36^\circ\text{C}$; $P = 0.037$), while control snakes' mean T_b ($19.18 \pm 1.73^\circ\text{C}$, $P = 0.09$) did not differ from translocated animals on this day. Confidence intervals for model-estimated mean T_b of each group overlapped in all other weeks of the study. Qualitative inspection of hourly temperature profiles of translocated, handled, and control snakes during week one of the study suggested that three translocated snakes did not re-emerge from burrows post-translocation, despite translocations occurring midday, a fact that could explain their low mean T_b during the 24 hr following translocation. Figure 4 shows such profiles for a representative snake from each treatment group during week one. Post-translocation, a rapid drop in T_b was incurred by the translocated animal, potentially due to hiding in a burrow for the duration of the day. However, an apparently normal T_b profile is taken up the following day. We were unable to find noticeable trends such as this during the following weeks of the study, and low sample size and variable times of day for application of treatment prevented statistical analysis of whether or not translocation delays re-emergence from shelter. Variance in T_b 24 hr after treatment was not significantly affected by treatment group ($F_{2,15} = 0.14$, $P = 0.86$) or the time of day that treatment was applied ($F_{1,99} = 0.01$, $P = 0.94$). The repeated effect of week was significant in this reduced dataset as well, with decreasing variance in T_b as the study progressed ($F_{5,57} = 40.1$, $P < 0.001$), while week and group did not interact significantly ($F_{10,55} = 0.55$, $P = 0.84$). As before, mass was significant where larger snakes had less variable T_b ($F_{1,15} = 4.75$, $P = 0.046$).

DISCUSSION

Our study demonstrates that *C. o. oregonus* is robust to potential impacts of SDT on their thermal ecology. We found no chronic differences among treatment groups in weekly mean T_b and variance in T_b over the course of the 6-week study, so the existence of major adverse impacts of SDT on thermoregulation in rattlesnakes was not supported. We did detect an effect of translocation during the first week of the study only, where mean T_b was reduced in translocated snakes. This ephemeral impact seems to be explained by re-emergence from shelter post-translocation, which was delayed by a 1 day. Our results are congruent with Roe et al. (2010), who found that Northern Water Snakes (*Nerodia sipedon*) subjected to LDT maintained body temperature profiles similar to resident conspecifics. However, translocated Water Snakes showed increased movement, which resulted in high levels of mortality. Rattlesnakes used in this study did not suffer increased mortality during SDT. Further, translocation did not enact chronic effects on adrenocortical secretion of corticosterone (Holding et al., in press), as baseline corticosterone concentrations did not differ between first capture and the end of the study, and the acute rise in corticosterone following 1 hr in a cloth bag was the same among the three treatment groups. From a conservation perspective, the results of our study are encouraging, as yet another line of evidence, gleaned from semi-continuous monitoring of T_b , supports the robustness of snakes to the potentially adverse effects of frequent human interference with their natural movement patterns. Similarly, Sartorius et al. ('99) documented that the thermal ecology of the Giant Ameiva (*Ameiva ameiva*) was unaffected in disturbed sites, and that these lizards actually showed a preference for anthropogenically-altered areas. Because thermoregulatory capacity is a key life history feature of ectotherms (reviewed in Angilletta et al., 2002), our study fills a major gap in the literature evaluating the efficacy of translocation programs.

We were able to further specify the timing of the week by treatment group interaction impacting mean T_b by modeling mean T_b during the day and night separately, and during the 24 hr immediately following the application of treatment. Thus, we demonstrate the importance of partitioning T_b variance into times dominated by behavioral thermoregulation versus those largely impacted by ambient temperature fluctuations and shelter quality. Specifically, translocated snakes experienced lower mean T_b immediately after translocation during the first week of the study only when compared to handled snakes, but not control snakes. The same was true for analysis of daytime, but not nighttime, mean T_b , suggesting that an acute impact of translocation is a lengthier duration of hiding below ground after translocation. As nighttime ambient temperatures are lower earlier in the year in Central California (Lobell et al., 2007), it is encouraging that the lower mean T_b observed during week one were localized to the daytime hours, suggesting that translocation is not impacting the ability of snakes to seek appropriate thermal refugia overnight. Belliure et al. (2004) documented altered behavioral activity and

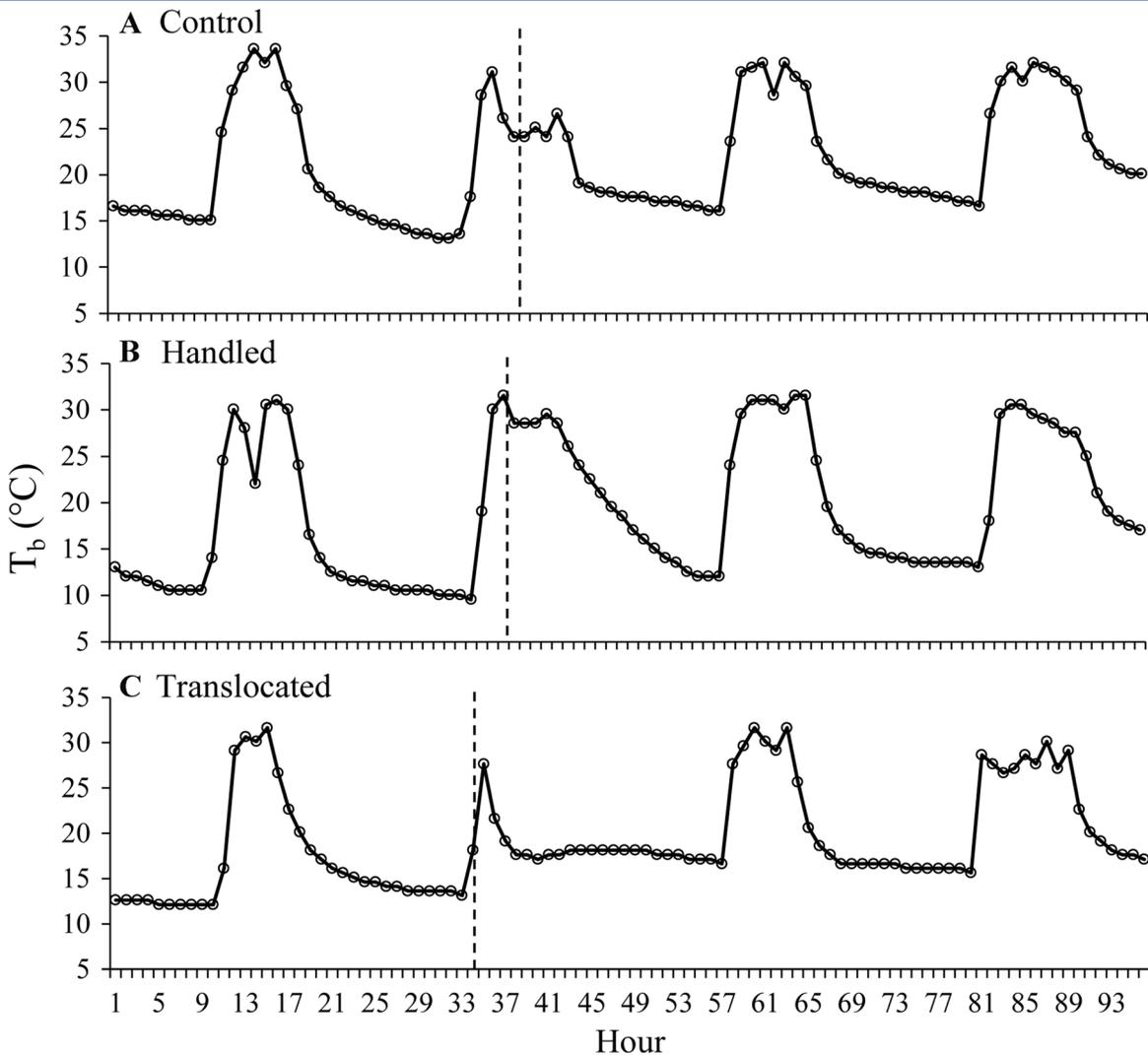


Figure 4. Hourly body temperatures (T_b) taken over a 96 hr period (30 April–3 May, 2010) for a representative control (A; top), handled (B; middle), and translocated (C; bottom) *Crotalus oreganus oreganus*. Vertical dashed lines in panels show the time when the snake was located (A) or when respective treatments were applied (B and C). While the handled animal (B) appears to have resumed above-ground activity post-handling, the translocated animal appears to have remained underground in the burrow to which it was relocated, resulting in a steep decrease in T_b for a day.

thermoregulation in juvenile Common Lizards (*Lacerta vivipara*) with experimentally elevated corticosterone levels, where lizards exposed to both prenatal and postnatal elevations in corticosterone were both shown to have increased activity and thermoregulatory behavior. As Holding et al. (in press) found no impact of translocation on adrenocortical secretion during acute handling stress in these same snakes, any explanation involving differential “stressfulness” of the experiences leading to different thermoregulatory behaviors afterward also seems unlikely.

We find the most likely explanation for lower mean T_b in translocated snakes during the daytime hours to be that trans-

located snakes remained below ground in the shelters to which they were translocated more frequently, possibly because they were in a new site, unlike handled controls. This behavior was localized to the first week and disappeared later in the study. The qualitative difference in temperature profiles among groups (Fig. 3), where T_b of translocated snakes takes a midday dive and remains low until the following morning, supports this “extended hiding” hypothesis. Future studies could employ automated temperature-based activity estimation (TBAE) to empirically test this hypothesis (Davis et al., 2008). This technique allows for the estimation of activity times and patterns in free-ranging

organisms, via the synchronization of T_{air} and T_{b} temporally plotted together on the same graph. While this technique's accuracy is not as high for rattlesnakes as it is for some other taxa, it nonetheless provides a means to use T_{b} to quantify the activity time(s) of free-ranging ectotherms. If snakes ceased extended hiding after week one, they may have acclimatized to the acute stress of translocation to some extent. A second, non-mutually exclusive explanation, is that these male snakes were driven to increased movement (and thus less thermoregulation) the day after translocation in response to the behavioral demands of the mating season. Mating activity begins in March, peaks in April, and wanes in early May for this population of *C. o. oreganus* (Lind et al., 2010), so the first week of treatment likely corresponded to the tail-end of mating activity. During the first 2 weeks of the study, males in the translocated group were moved away from females they were courting, and these snakes were the only animals to return to the site from which they were translocated by the next day of radio-tracking (Holding et al., in press). The lack of nocturnal temperature differences among treatment groups and the thermal profiles of the snakes do not support nocturnal return across the 225 m back to the females, so a rapid return the morning after translocation could have been their mode of return to the females. As shown in Fig. 3, mean daytime T_{b} during the first 2 weeks was actually higher than mean highs for air temperature. Thus, snakes were behaviorally elevating temperatures by basking, an activity that translocated animals may have had less time for because they had to first move back toward females. Concerning the efficacy of SDT for rattlesnakes, we suggest that such an ephemeral effect on T_{b} is minor (1–2°C following the first of six translocations only) and demonstrates the resilience of snakes to frequent encounters with humans, even on timescales as fine as a few days. Since female reptiles have greater thermoregulatory requirements (Shine, '80), and therefore may be more sensitive to alterations in their thermal ecology, additional studies should address the effects of SDT on female rattlesnakes, especially in pregnant animals.

Our study also documented the influence of body mass on the thermal biology of *C. o. oreganus*. Larger snakes had less variation in T_{b} than smaller conspecifics. Larger body size provides a lower surface area to volume ratio and therefore increased thermal inertia, retarding cooling rates. Ayers and Shine ('97) showed that body size significantly affects the cooling rates of Diamond Python (*Morelia spilota*), and consequently the ability to detect prey (via tongue flicking). Hatchling and juvenile pythons had much higher rates of cooling, resulting in decreased foraging time and a decreased ability to detect potential prey. Because of their higher cooling rates, hatchling and juvenile snakes may be more susceptible to the thermal impacts of translocation than adults. Studies that evaluate translocation efficacy in areas characterized by more extreme temperature swings than those in Central California may wish to consider comparing the success of moving large versus small animals while recording body temperature.

Our results support the notion that body size should be incorporated into investigations of the thermal ecology of ectotherms in general.

To our knowledge, this is the only study to examine the direct thermal impacts of repeated SDT on an organism. This paucity of data has effectively limited the capacity of potential conservation and management efforts. With many rattlesnakes suffering broad-scale declines, including the Eastern Massasauga (*Sistrurus catenatus catenatus*; Gibbs et al., '97), Timber Rattlesnake (*Crotalus horridus*; Brown, '93), and Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*; Waldron et al., 2008), studies are needed to ascertain the effects of translocation at the interface of physiology and behavior. The primary concern with SDT is the potential return of translocated snakes, where they could once again have negative interactions with humans (Hardy et al., 2001; Brown et al., 2009; Holding et al., in press). While a valid concern, we argue that this is a minor problem. The likelihood of a translocated individual being spotted again by the general public is small. Indeed, translocated individuals can be relatively difficult to detect, even by experienced investigators (Brown et al., 2009). Consequently, while the act of SDT may not completely remove the probability of the snake reencountering a human, SDT provides a safe alternative for the snake(s), eliminates immediate human–snake conflict, and provides peace of mind to the public. Future studies should investigate the effect on thermoregulation of LDT, which prevents snakes from returning to the sites of capture but may be more stressful to the snakes because they are moved far outside of familiar territory.

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LITERATURE CITED

- Aïdam A, Michel CL, Bonnet X. 2013. Effects of ambient temperature in neonate aspik vipers: growth, locomotor performance, and defensive behaviors. *J Exp Zool* 319A:310–318.
- Angilletta MJ, Niewiarowski PH, Navas CA. 2002. The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268.

- Ayers DY, Shine R. 1997. Thermal influences on foraging ability: body size, posture and cooling rate of an ambush predator, the python *Morelia spilota*. *Funct Ecol* 11:342–347.
- Belliure J, Meylan S, Clobert J. 2004. Prenatal and postnatal effects of corticosterone on behavior in juveniles of the common lizard, *Lacerta vivipara*. *J Exp Zool* 301A:401–410.
- Besson AA, Cree A. 2011. Integrating physiology into conservation: an approach to help guide translocations of a rare reptile in a warming environment. *Anim Conserv* 14:28–37.
- Brown WS. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. *Herpetol Circ* 22:1–78.
- Brown JR, Bishop CA, Brooks RJ. 2009. Effectiveness of short-distance translocation and its effects on western rattlesnakes. *J Wildl Manag* 73:419–425.
- Butler H, Malone B, Clemann N. 2005. The effects of translocation on the spatial ecology of tiger snakes (*Notechis scutatus*) in a suburban landscape. *Wildl Res* 32:165–171.
- Cree A, Tyrell CL, Preest MR, Thorburn D, Guillette LJ. 2003. Protecting embryos from stress: corticosterone effects and the corticosterone response to capture and confinement during pregnancy in a live-bearing lizard (*Hoplodactylus maculatus*). *Gen Comp Endocrinol* 134:316–329.
- Davis JR, Taylor EN, DeNardo DF. 2008. An automated temperature-based option for estimating surface activity and refuge use patterns in free-ranging animals. *J Arid Environ* 72:1414–1422.
- Dickens MJ, Delehanty DJ, Romero LM. 2010. Stress: an inevitable component of animal translocation. *Biol Conserv* 143:1329–1341.
- Dodd CK, Seigel RA. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? *Herpetologica* 47:336–350.
- Dunlap KD, Wingfield JC. 1995. External and internal influences on indices of physiological stress I. Seasonal and population variation in adrenocortical secretion of free-living lizards, *Sceloporus occidentalis*. *J Exp Biol* 271:36–46.
- Fischer J, Lindenmayer DB. 2000. An assessment of the published results of animal relocations. *Biol Conserv* 96:1–11.
- Gardner-Santana LC, Beaupre SJ. 2009. Timber rattlesnakes (*Crotalus horridus*) exhibit elevated and less variable body temperatures during pregnancy. *Copeia* 2009:363–368.
- Gibbs H, Prior K, Weatherhead P, Johnson G. 1997. Genetic structure of populations of the threatened eastern massasauga rattlesnake, *Sistrurus c. catenatus*: evidence from microsatellite DNA markers. *Mol Ecol* 6:1123–1132.
- Hardy DL, Greene HW, Tomberlin B, Webster M. 2001. Relocation of nuisance rattlesnakes: problems using short-distance translocation in a small rural community. *Sonoran Herpetol* 14:1–3.
- Holding ML, Frazier JA, Taylor EN, Strand CR. 2012. Experimentally altered navigational demands induce changes in the cortical forebrain of free-ranging Northern Pacific rattlesnakes (*Crotalus o. oreganus*). *Brain Behav Evol* 79:144–154.
- Holding ML, Frazier JA, Dorr SW, Henningsen SN, Moore IT, Taylor EN. 2014. The physiological and behavioral effects of repeated handling and short distance translocation on free-ranging northern Pacific rattlesnakes (*Crotalus oreganus oreganus*). *J Herpetol* 48:000–000. doi: 10.1670/11-314.
- Kaufmann JS, Bennett AF. 1989. The effect of temperature and thermal acclimation on locomotor performance in *Xantusia vigilis*, the desert night lizard. *Physiol Zool* 62:1047–1058.
- Lind CM, Husak JF, Eikenaar C, Moore IT, Taylor EN. 2010. The relationship between plasma steroid hormone concentrations and the reproductive cycle in the Northern Pacific rattlesnake, *Crotalus oreganus*. *Gen Comp Endocrinol* 166:590–599.
- Lobell DB, Cahill KN, Field CB. 2007. Historical effects of temperature and precipitation on California crop yields. *Clim Chang* 81:187–203.
- Madsen T, Shine R, Olsson M, Wittzell H. 1999. Restoration of an inbred adder population. *Nature* 402:34–35.
- McLachlan JS, Hellmann JJ, Schwartz MW. 2007. A framework for debate of assisted migration in the era of climate change. *Conserv Biol* 21:297–302.
- Nowak EM, Hare T, McNally J. 2002. Management of "nuisance" vipers: effects of translocation on western diamond-backed rattlesnakes (*Crotalus atrox*). In: Schuett GW, Hoggren M, Douglas ME, Greene HW, editors. *Biology of the vipers*. USA: Eagle Mountain Publishing. p 533–560.
- Putman BJ, Lind C, Taylor EN. 2013. Does size matter? Factors influencing the spatial ecology of northern pacific rattlesnake (*Crotalus oreganus oreganus*) in Central California. *Copeia* 2013:485–492.
- Reinert HK, Rupert RR Jr. 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. *J Herpetol* 33:45–61.
- Roe JH, Frank MR, Gibson SE, Attum O, Kingsbury BA. 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. *J Appl Ecol* 47:1253–1261.
- Row JR, Blouin-Demers G. 2006. Thermal quality influences effectiveness of thermoregulation, habitat use, and behaviour in milk snakes. *Oecologia* 148:1–11.
- Sartorius SS, Vitt LJ, Colli GR. 1999. Use of naturally and anthropogenically disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biol Conserv* 90:91–101.
- Seddon PJ, Armstrong DP, Maloney RF. 2007. Developing the science of reintroduction biology. *Conserv Biol* 21:303–312.
- Shine R. 1980. "Costs" of reproduction in reptiles. *Oecologia* 46:92–100.
- Taylor EN, DeNardo DF, Malawy MA. 2004. A comparison between point- and semi-continuous sampling for assessing body temperature in a free-ranging ectotherm. *J Therm Biol* 29:91–96.
- Waldron JL, Welch SM, Bennett SH. 2008. Vegetation structure and the habitat specificity of a declining North American reptile: a remnant of former landscapes. *Biol Conserv* 141:2477–2482.

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