No place like home: an experimental comparison of reintroduction strategies using snakes

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Summary

1. The practice of deliberately moving animals from one site to another for conservation is increasing as a tool to re-establish extirpated populations. Resource managers are faced with developing strategies for reintroduction attempts, but often lack experimentally derived evidence upon which to base decisions.

2. Using the northern water snake Nerodia sipedon sipedon in the USA, we compared the behaviour and performance of resident snakes with that of individuals translocated directly from the wild to a nearby nature reserve or reared in captivity prior to translocation.

3. Both translocated groups had low survivorship relative to resident snakes, but the proximal causes of their poor performance differed considerably. Captive-reared snakes exhibited restricted surface activity and movements and abnormal habitat use, and ultimately failed to maintain appropriate body temperature and body mass, with high mortality associated with the overwintering period. Wild snakes directly translocated to an unfamiliar site maintained body temperatures and growth comparable with residents, but their more extensive movements resulted in frequent excursions off reserve and high mortality.

4. Synthesis and applications. We contend that an individual's prior experience is an important factor in determining their behaviour and performance during the phase of early establishment at an unfamiliar site. This suggests the existence of common underlying mechanisms influencing the outcome of reintroduction attempts, and provides a potentially useful framework for improving reintroduction efforts. Resource managers would likely improve success of reintroductions by matching habitats (and associated resources and conditions) between source and release sites, by temporarily confining animals in enclosures that force new associations to be made while limiting exploratory wanderings, or by enrichment of environmental conditions in captivity.

Key-words: captive breeding, head-starting, natal habitat preference induction, Nerodia sipedon, radio-telemetry, repatriation, reptile, restoration, survival probability, translocation

Introduction

The practice of moving animals for conservation or wildlife management purposes is increasing (Seddon, Armstrong & Maloney 2007). There are several reasons why resource managers may attempt animal translocation, defined as the deliberate movement of individuals from one part of their distribution to another where the species historically occurred or is currently present (IUCN 1998). Animals may be removed from an area due to imminent threats to their survival (Tuberville et al. 2005; Griffiths & Pavajeau 2008), to mitigate conflicts (Sullivan, Kwiatkowski & Schuett 2004; Bradley et al. 2005), to assist colonization in response to climate change (McLachlan, Hellmann & Schwartz 2007), to introduce genetic variation (Madsen et al. 1999), or for population re-establishment (Pedrono & Sarovy 2000; Moorhouse, Gelling & MacDonald 2009). Several of these examples are typically part of larger conservation efforts to re-establish faunal populations or augment existing ones at sites that have been restored to address threats to the species’ or population’s persistence.

Attempts to reintroduce animals often fail to result in the establishment of viable populations for numerous reasons...
reviewed elsewhere (Dodd & Seigel 1991; Fischer & Lindenmayer 2000). This limited success has led to the development of many novel techniques for reintroduction programmes and calls for the application of more scientifically rigorous approaches to addressing problems (Fischer & Lindenmayer 2000; Seddon et al. 2007; Armstrong & Seddon 2008; Kingsbury & Attum 2009). In its simplest form, animals can be captured from one site and immediately released into another, but several manipulations may improve the likelihood of success. For instance, the identification of appropriate source populations and use of captive-breeding, along with modifications to the demography of release cohorts, the timing of their release, and use of temporary enclosures to acclimate and familiarize animals to site conditions are some examples of methods that have proven useful (Bright & Morris 1994; Sarrazin & Legendre 2000; Tuberville et al. 2005; Griffiths & Pavajeau 2008). An experimental approach to developing the most appropriate ‘recipe’ for reintroduction has led to some recent successes in translocation programmes, providing encouraging evidence that translocation can be a useful conservation tool (Taylor, Jamieson & Armstrong 2005; Griffiths & Pavajeau 2008; Germano & Bishop 2009; Santos et al. 2009).

Here, we experimentally test the feasibility of common reintroduction strategies by assessing the post-release behaviour, body temperature, growth and survival (collectively referred to as performance measures hereafter) of northern water snakes Nerodia sipedon sipedon (Linnaeus) translocated under different scenarios in the USA. One group was raised in captivity at accelerated growth rates throughout an early part of their life cycle prior to release in the wild – a strategy known as head-starting (Pritchard 1979). The other consisted of snakes captured and immediately translocated to an unfamiliar site without captive-rearing – a strategy we refer to as direct translocation. Head-starting works on the assumption that by releasing animals into the wild at a larger size, when they are presumably less vulnerable to predation and closer to reproductive maturity, the reintroduced animals will have a higher probability of establishing a population. When combined with captive-breeding programmes, head-starting can also be used to arrange for multiple releases of numerous individuals with less stress on wild donor populations (Brown & Day 2002). The direct translocation of wild-caught animals represents a simpler (and perhaps cheaper) alternative to head-starting, assuming wild stock can still be attained without jeopardizing donor population viability (Dimond & Armstrong 2007). We add an additional layer of comparisons by studying snakes already residing in the release site, which serve as reference benchmarks against which to gauge the performance of the experimental release groups.

The goal of this study is not to attempt a population re-establishment (see Seddon 1999). Instead, we take an alternative approach by intensively monitoring the post-release behavioural responses (e.g. movements, activity and habitat selection) and subsequent consequences (temperature regulation, vital rates) for several individuals during the early process of establishment at unfamiliar sites. This design allows us to test two central (yet unresolved) questions in reintroduction biology: (i) what impact does a period of captive-rearing have on the performance of snakes during early establishment at unfamiliar sites in the wild, and (ii) how do translocated individuals (captive-reared or not) perform relative to snakes already residing in the release site? This approach can lead to a better understanding of the mechanistic basis for a particular manipulation’s outcome, providing valuable information on how to cautiously proceed with and improve translocation efforts.

Materials and methods

STUDY SITE AND MAPPING

Snakes were studied from June 2008 to June 2009 in northeast Indiana, USA, at an c. 500 ha nature reserve managed by The Nature Conservancy. The core terrestrial habitat of the reserve consists primarily of hardwood forests interspersed with several old field or scrub-shrub patches, many of which have been recently replanted for reforestation. Scattered throughout the reserve are numerous water bodies, several of which have been restored or created in ongoing site restoration efforts. The study area is bordered by a creek, and the adjacent private lands are predominantly used for agriculture and low-density housing residences.

Maps describing the distribution of macro-habitats in the study area were digitized from aerial photographs using ArcGIS 9.3 (ESRI 2008). Habitat types were defined based on Cowardin et al. (1979): palustrine open (PO) – wetlands dominated by open water and/or herbaceous emergent vegetation; palustrine scrub-shrub/forested (PSS/PFO) – wetlands dominated by trees and/or shrubs; and river/stream (RIV) – an area of flowing water confined to the channel. Upland habitats (i.e. those outside of typical flood zones) were defined as upland forest (UFO) – areas dominated by tree canopy cover; old field/upland scrub-shrub (OF/USS) – primarily open habitats dominated by grasses, forbs, or low shrubby vegetation; and agricultural/residential (AG/RES) – areas actively maintained for agricultural or residential purposes.

ANIMAL CAPTURE, MAINTENANCE, AND RADIO-TRANSMITTER IMPLANTATION

In July 2007, seven pregnant N. s. sipedon were captured from a site c. 5 km north of the study area and allowed to give birth in the laboratory at Indiana-Purdue University in Fort Wayne, Indiana, USA. Sixty neonates (30 male and 30 female) were retained and raised in captivity, whereas adult females and remaining neonates were immediately returned to their sites of capture. Captive snakes were housed individually in small plastic boxes (20 × 65 × 13 cm) with access to a hide box and water bowl, with heat tape providing a thermal gradient on the floor of the box. The room temperature was set at 25°C, relative humidity typically remained between 30% and 60%, and lights were set to a 12L : 12D cycle. Snakes were fed several live fish 2–3 times per week. These husbandry practices were maintained throughout the entire 11-month-captive period in an effort to accelerate growth rates and maximize size and survivorship for release the following summer. Thus, no cooler overwintering period was employed. At the end of the captive period, 12 snakes, representing offspring of seven females, were selected for release. We did not select snakes randomly because we were limited to using only those large enough for transmitter implantation (see Table 1). We refer to this study group as ‘head-starts’ hereafter.

Table 1. Details of the three treatment groups upon release

<table>
<thead>
<tr>
<th>Group</th>
<th>n</th>
<th>Sex ratio (F:M)</th>
<th>Snout-to-vent length (cm)</th>
<th>Transmitter weight (% of snake body mass)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head-start</td>
<td>12</td>
<td>9:3</td>
<td>47.3 ± 2.2 (43.1–49.8)</td>
<td>5.9 ± 0.6 (5.2–7.0)</td>
</tr>
<tr>
<td>Resident</td>
<td>12</td>
<td>9:3</td>
<td>51.3 ± 2.9 (46.7–55.6)</td>
<td>5.4 ± 1.0 (3.9–7.2)</td>
</tr>
<tr>
<td>Translocation</td>
<td>10</td>
<td>6:4</td>
<td>57.1 ± 9.9 (47.3–77.5)</td>
<td>3.7 ± 1.9 (1.2–7.0)</td>
</tr>
</tbody>
</table>

Values are mean ± 1 SD and (range).

In May 2008, we captured 12 snakes from the study area and 10 snakes from the same source population as the head-starts. Snakes captured from the study area are referred to as ‘residents’ hereafter, and those captured from the same property as the head-starts, but not raised in captivity, are referred to as the ‘translocation’ group hereafter. Snakes in all three groups (i.e. head-start, resident and translocation) were surgically implanted with radio-transmitters (model SB-2T, 51 g; Holohil Systems Ltd, Carp, ON, Canada) while under anaesthesia using a technique described in Roe, Kingsbury and Herbert (2003). We attempted to match the body size, sex composition and numbers of individuals in the three groups as closely as possible (Table 1). After a 7- to 11-day recovery from surgery, resident snakes were released in their wetland of capture, along-side an approximately equivalent number of snakes from the experimental release groups.

FIELD DATA COLLECTION

We located snakes at least once per week during the active season (May–September), every 2 weeks around the times of hibernation ingress (October–November) and egress (March–April), and once per month for the remainder of the overwintering period (December–February). At each radio-location, we determined the coordinate position using GPS held at the snake’s location. GPS units typically had an error of less than 7 m. We then plotted location coordinates using ArcGIS 9.3. We also determined the macro-habitat type in which the snake was located and attempted to make a visual observation of the individual to confirm its status as alive or dead, and whether it was active above the surface, in the water, or buried under vegetation, debris, or in a burrow. If a snake was confirmed dead after an extended period below-ground or water in the same location, then we presumed it had been dead since the last confirmed visual observation or movement.

Several additional variables were derived to describe the behaviour and performance of each snake. We calculated minimum convex polygons (MCP) to estimate the size of area used with the Hawth’s Tools extension in ArcGIS, and measured linear range length as the straight-line distance between the two most widely spaced radio-locations. MCPs and range lengths were calculated using all active season locations and one overwintering location. Movement distances were measured as the straight-line distance between two sequential locations. A monthly index of surface activity was calculated as the proportion of radio-locations where the snake was visually confirmed on the surface as basking, foraging, mating, travelling or fleeing. Transmitter pulse rates were recorded and converted to temperature (to the nearest 0.1 °C) using calibration curves provided by the manufacturer. We periodically captured snakes and measured their snout-to-vent length (SVL); to the nearest 0.1 cm and mass (to the nearest 0.1 g) using fabric tape and an electronic balance. The date of hibernation ingress was the final day of confirmed surface activity in autumn, and hibernation egress was the first date of known spring activity.

DATA ANALYSES

We performed statistical analyses with sas 17.0 (SPSS 2007), the program mark 5.0 (White & Burnham 1999) and Compos Analysis 6.2 (Smith 2004). Where appropriate, we examined the assumptions of homogeneity of variances and normality; when data failed to meet assumptions, they were transformed to approximate normal distributions or equal variances. Statistical significance was accepted at the α ≤ 0.05 level except for multiple related comparisons, where the Dunn-Sidak method was applied to constrain the experiment-wide Type I error to 0.05 (Quinn & Keough 2002). In all analyses, sexes were pooled within treatments to increase sample sizes and power.

We used a multivariate analysis of covariance (MANCOVA) to test for the effects of treatment group on movement rate (log_{10} m/day) and size of area used (log_{10} MCP), with log_{10} SVL and number of radio-fixes as covariates. Mean monthly surface activity indices (arc-sine-transformed) were examined using analysis of covariance (ANCOVA), with treatment group as the predictor variable and time of day as a covariate. The Dunn-Sidak adjusted level of significance for this series of surface activity tests was 0.010. Variation among groups in dates of hibernation ingress and egress were examined with Mann-Whitney tests, using Julian day counted from 1 January as the dependent variable.

We used compositional analysis to investigate habitat selection (Aebischer, Robertson & Kenward 1993). Habitat selection was assessed by comparing the relative proportions of habitats used by the individual to the habitats’ relative availability on the site. Habitats that were not used were replaced with a value of 0.7%; which was identified as minimizing misclassification error rates (Bingham, Brennan & Ballard 2007). The study site was defined as the MCP drawn around the combined positions for snakes in all three treatment groups.

Body temperature (T_b) and time of location were compiled into monthly mean values for each individual. We then used ANCOVA to test for the effects of treatment on T_b for each month separately, using time of day as a covariate. The Dunn-Sidak adjusted level of significance for this series of T_b tests was 0.010. Body condition indices (BCI) at time of release were compared among groups using the method described by Beaupre & Douglas (2009). BCI was estimated as the deviation in observed mass from that predicted by the regression relationship between body mass and SVL of all snakes. BCIs were then compared using ANCOVA. ANCOVA was used to test for treatment differences in growth rates, using log_{10} g/day as the dependent variable and log_{10} initial SVL as the covariate.

Survival probabilities were estimated using known fate models in the program mark. Time periods when radio-signals could not be detected (i.e. transmitter failure or undetected long-distance movements) were censored from the analysis. Akaike information criterion (AIC) was used to rank candidate models; if competing models had AIC values of < 2.0, they were considered as having some support. Time intervals were set as bi-weekly during the active season and condensed into a single period during hibernation. We defined the
Movement rates and size of area used differed among treatment groups, with translocated snakes exhibiting the highest vagility and head-starts the lowest (Tables 2 and 3). Head-starts were also less active on the surface than residents and translocated snakes in both June and July (\( P \leq 0.001 \) in both cases), but not from August to October (\( P > 0.064 \) in all cases; Fig. 1). Information on hibernation ingress and egress could be obtained for only one translocated snake, so we went forward with analyses of head-started and resident snakes only. Dates of hibernation ingress were similar between treatment groups, with entrance dates of 8 November ± 3 days (mean ± 1 SE) for eight head-starts and 7 November ± 3 days for seven residents (\( Z = -0.495, P = 0.694 \)). Mean dates of hibernation egress differed between treatments groups, with seven head-starts initiating spring activity on 17 March ± 0.4 days, and seven residents becoming active on 21 April ± 0.2 days (\( Z = -3.25, P = 0.001 \)).

**Results**

**MOVEMENTS AND ACTIVITY**

Fig. 1. Monthly surface activity for resident (Res), head-started (Hst), and directly translocated (Tra) water snakes. The surface activity index is the mean (± 1 SE) proportion of radio-fixes where the presence of a snake on the surface was confirmed visually as either basking, foraging, mating or travelling. Number of snakes in each treatment group (head-start, resident, translocated) are as follows: June (4, 6, 4), July (11, 12, 10), August (11, 11, 9), September (11, 9, 6), October (11, 7, 3).

**HABITAT SELECTION**

We limited analyses to the four primary habitats used by the snakes, including palustrine open, palustrine scrub-shrub/forested, upland forest and old field/upland scrub-shrub. More than 99% of snake locations were within these four habitat types that together represented >91% of the 160-ha study area. Treatment groups exhibited different patterns of habitat selection (Table 4, Fig. 2). Resident snakes selected palustrine open and scrub-shrub/forested wetlands equally, with little distinction between upland forest and old field/upland scrub-shrub habitats. Translocated snakes selected palustrine open wetlands over scrub-shrub/forested wetlands, and old field/upland scrub-shrub habitats over upland forests. Head-starts exhibited neither strong selection nor avoidance of any habitat type. Overall, head-starts spent c. 48% of the active season in terrestrial habitats compared with only 13–15% for resident and translocated snakes.

**Table 2. Movement and spatial variables for resident snakes compared with head-started and directly translocated experimental release groups**

<table>
<thead>
<tr>
<th>Group</th>
<th>( n )</th>
<th>Area used (ha)</th>
<th>Range length (m)</th>
<th>Movement distance (m per day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head-start</td>
<td>12</td>
<td>23 ± 1.3</td>
<td>198 ± 63</td>
<td>6.9 ± 20</td>
</tr>
<tr>
<td>Resident</td>
<td>12</td>
<td>48 ± 1.7</td>
<td>390 ± 82</td>
<td>16.7 ± 34</td>
</tr>
<tr>
<td>Translocated</td>
<td>10</td>
<td>133 ± 3.9</td>
<td>707 ± 139</td>
<td>22.6 ± 30</td>
</tr>
</tbody>
</table>

Values are mean ± 1 SE.

**Table 3. Results of MANOVA for the effects of number of radio-fixes, body size [snout-to-vent length (SVL)] and treatment on movements and spatial ecology of water snakes experimentally introduced to an unfamiliar location**

<table>
<thead>
<tr>
<th>Effect</th>
<th>Wilks’ Lambda</th>
<th>Num d.f.</th>
<th>Den d.f.</th>
<th>( F )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radio-fixes</td>
<td>0.331</td>
<td>2</td>
<td>25</td>
<td>25.21</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SVL</td>
<td>0.990</td>
<td>2</td>
<td>25</td>
<td>0.122</td>
<td>0.866</td>
</tr>
<tr>
<td>Treatment</td>
<td>0.484</td>
<td>4</td>
<td>50</td>
<td>5.67</td>
<td>0.001</td>
</tr>
</tbody>
</table>

Common superscripts within a row indicate habitats that were ranked similarly.

*Habitats include palustrine scrub-shrub/forest mix (PSS/PFO), palustrine open (PO), upland forest (UFO), and old field/upland scrub-shrub mix (OF/US). See text for habitat descriptions.
BODY TEMPERATURE, BODY CONDITION INDEX AND GROWTH

After accounting for variation in time of day, $T_b$ of the head-starts was lower than the resident and translocated groups from June to August ($P \leq 0.045$ in all cases), but not from September to October ($P \geq 0.195$ in both cases; Fig. 3). Initial BCIs were lowest in residents ($-124 \pm 46$), intermediate in head-starts ($41 \pm 18$) and highest in translocated snakes ($166 \pm 46$; ANOVA: $F_{2,31} = 14.18$, $P < 0.001$). We were able to recapture ten head-starts, 11 residents, and eight translocated snakes for growth measurements. Growth rates measured as change in mass and length were correlated ($r^2 = 0.56$, $P < 0.001$). After accounting for variation in SVL, growth rates of head-starts were lower than for resident and translocated snakes (SVL: $F_{1,25} = 16.46$, $P < 0.001$; treatment: $F_{2,25} = 3.56$, $P = 0.044$; Fig. 4).

SURVIVORSHIP AND OFF-SITE EXCURSIONS

In our probative model, we found little evidence that survival probability varied over time (AICc $> 2$), so we went forward with simpler models examining variation among treatment groups and body sizes, holding time constant. The model with the most support identified residents as having higher survival probabilities than translocated and head-started snakes, though models with constant survival among groups and head-starts with the lowest survival also had some support (Table 5). Bi-weekly survival probabilities were $0.961 \pm 0.017$, $0.922 \pm 0.033$ and $0.912 \pm 0.030$ for resident, translocated and head-started snakes, respectively, corresponding to annual survival rates of 45.2%, 19.6% and 16.0%. Groups differed in their propensity to leave the nature reserve boundaries, with 40% of translocated snakes leaving the reserve compared with 8% for head-starts and 0% in residents ($P = 0.025$).

Discussion

The ultimate success of an animal reintroduction programme hinges first upon the short-term performance of individuals in an unfamiliar environment. Reintroduced animals must adopt behaviours suitable for the release site such that they can

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**Fig. 2.** Comparison of habitat selection for resident (Res), head-started (Hst) and directly translocated (Tra) water snakes. The habitat selection index was derived by subtracting the proportion of available habitat from proportion of habitats used by individuals. Habitats used more frequently than their availability (i.e. selected) are shown as positive, and those used less frequently than their availability (i.e. avoided) are shown as negative. See text for description of habitat types.

**Fig. 3.** Monthly day-time body temperatures ($T_b$) of resident (Res), head-started (Hst) and directly translocated (Tra) water snakes. Values are mean ± 1 SE. Refer to Fig. 1 for sample sizes in each month.

**Fig. 4.** Growth rates measured in (a, cm per day), and (b, g per day) for resident (Res), head-started (Hst) and directly translocated (Tra) water snakes. Values are mean ± 1 SE.

maintain homeostasis, avoid predators, find shelter, forage, grow, survive the initial reintroduction period and establish some degree of site fidelity. Although not indicators of a successful reintroduction themselves, these are all prerequisite to the breeding and eventual persistence of the re-established population (Kleiman 1989; Stamps & Swaisgood 2007). We found marked differences in the movement, activity and habitat selection behaviours of our experimental release groups, as well as variation in important physiological consequences and vital rates including temperature regulation, growth and survivorship. The most important findings relevant to reintroduction programmes were that (i) head-started and translocated snakes performed relatively poorly compared with residents, (ii) the proximal causes underlying the performance of experimentally reintroduced snakes differed considerably, and (iii) the performance of reintroduced snakes appears to relate ultimately to the snake’s prior experience, this last point suggesting a common underlying mechanism and framework for improving reintroduction efforts.

**Reintroduced Compared with Resident Snakes**

We addressed the concerns of whether the use of captive-bred or wild-caught snakes translocated to an unfamiliar site compromises an individual’s ability to behave appropriately and survive their first year in the wild. Head-starts moved considerably less and traversed smaller areas than either of the other groups. Perhaps most strikingly, head-starts demonstrated little motivation (or ability) to select or avoid habitats in a manner consistent with other water snakes. As a result, head-starts spent nearly half of their active season in terrestrial habitats, which is uncharacteristic of *N. sipedon* (Roe, Kingsbury and Herbert 2003). Moreover, head-starts were rarely observed basking, foraging or travelling, all of which were surface activities commonly observed in resident snakes, and they exited hibernation refuges c. 1 month prior to resident snakes. As a consequence, head-starts were less likely to make exploratory movements, had active season $T_a$ considerably cooler than that preferred by *N. sipedon* (Brown & Weatherhead 2000), failed to gain weight, and had high rates of mortality.

Wild-caught snakes directly translocated to unfamiliar environments also behaved abnormally with respect to residents. Translocated snakes moved more extensively and frequently used areas outside of reserve boundaries. Translocated snakes selected open canopied wetlands over scrubby or forested wetlands, whereas resident wild snakes selected both wetland types equally. However, translocated snakes largely avoided terrestrial habitats, remained active on the surface throughout the active season, maintained active season $T_a$ within the preferred range of *N. sipedon* (Brown & Weatherhead 2000), and grew appreciably, though mortality rates were higher than resident snakes.

**Proximal Causes of Performance Variation**

Although survival was relatively low in both reintroduction groups, the proximal causes underlying performance variation differed considerably. Although our models did not detect significant variation in survival over time, there is evidence that head-starts did experience relatively high (and perhaps biologically significant) mortality associated with the overwintering period. From November to March, only 50% of head-starts survived compared with 100% in both other groups (Fig. 5). One head-start never emerged from its burrow, and the other three were found dead in the vicinity of their hibernation refuges shortly after they emerged, but before any of the resident snakes initiated spring activity. It is possible that the head-starts’ poor nutritional state led them to premature emergence and exposure to cold temperatures and predators in early

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**Table 5. Models of survivorship probability (S) for resident snakes (RES) compared to head-start (HST) and translocated (TRA) experimental release groups. All models include initial body size as a covariate**

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Weight</th>
<th>$n$</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S = HST \geq TRA &gt; RES$</td>
<td>179-39</td>
<td>0</td>
<td>0.06</td>
<td>3</td>
<td>173-33</td>
</tr>
<tr>
<td>$S = TRA \geq HST \geq RES$</td>
<td>180-47</td>
<td>1.07</td>
<td>0.21</td>
<td>2</td>
<td>176-43</td>
</tr>
<tr>
<td>$S = TRA \geq RES \geq HST$</td>
<td>180-68</td>
<td>1.29</td>
<td>0.19</td>
<td>3</td>
<td>174-62</td>
</tr>
<tr>
<td>$S = RES \geq TRA \geq HST$</td>
<td>181-41</td>
<td>2.01</td>
<td>0.13</td>
<td>4</td>
<td>173-30</td>
</tr>
<tr>
<td>$S = RES \geq HST \geq TRA$</td>
<td>181-85</td>
<td>2.84</td>
<td>0.11</td>
<td>3</td>
<td>175-78</td>
</tr>
</tbody>
</table>
spring, as has been observed in other natricine snakes (Alek-
suik & Stewart 1971; Brown & Weatherhead 1997; Shine et al.
2001). Mortality associated with overwintering could also
result from a poor choice of microsites or an inability to time
emergence with appropriate seasonal environmental cues.

In contrast, the poor performance of translocated snakes
most probably resulted from their extensive movements.
Wide-ranging movement is a common response to transloca-
tion, presumably as individuals search for familiar sites or
attempt to home (Reinert & Rupert 1999; Bright & Morris
2004; Sullivan et al. 2004; Butler, Malone & Clemann 2005;
Tuberville et al. 2005). Such movements resulted in high move-
ment rates and several snakes using areas outside of the nature
reserve, both of which are likely to increase a translocated ani-
mal’s exposure to predators and other threats (Meek et al.

ROLE OF PRIOR EXPERIENCE

A potential common mechanism underlying the post-release
behaviours of head-started and translocated snakes is natal
habitat preference induction (NHPI), a form of behavioural
plasticity whereby an individual’s earlier experience shapes
habitat preferences later in life (Davis & Stamps 2004). NHPI
theory predicts that when dispersing animals encounter unfa-
miliar environments, they will select habitats with cues resem-
bling those they are familiar with, assuming their prior
experience was positive (Davis & Stamps 2004; Stamps & Swais-
good 2007).

The early habitat experience of head-starts was limited to
simple, primarily terrestrial enclosures that offered few (if any)
similarities to natural environments. As predicted by NHPI
theory, head-starts failed to exhibit habitat selection or avoid-
ance – perhaps because there were no familiar habitat cues at
the release site. It is also possible that captive conditions may
have encouraged maladaptive behaviours in the wild. For
example, during captivity snakes heated via conduction from
the floor, whereas wild water snakes regulate Tb via solar radia-
tion during aerial basking or conductance in the water
(Brown & Weatherhead 2000). Not surprisingly, retreat into
subsurface burrows during the active season failed to translate
into high Tb for head-starts in the wild. In either case, the role
of prior experience provides a likely explanation for some of
the head-starts’ abnormal behaviours and poor performance
in the wild, a contention supported by numerous studies dem-
onstrating how conditions experienced in captivity influence
habitat choice, locomotor performance, problem-solving abil-
ity, exploration, and foraging in snakes (Almli & Burghardt
2006; Aubret & Shine 2008) and other animals (Davis &
Stamps 2004; Stamps & Swaisgood 2007).

Although we do not know for certain the early habitat ex-
periences of translocated snakes, all were captured from a com-
plex of open canopy wetlands surrounded by old field and
scrubby uplands. Consistent with NHPI, translocated snakes
demonstrated strong preference for open wetlands, a pattern
in contrast to the mixed use of wetland types (forested/scrub,
and open) by resident snakes. Translocated animals have been
shown to use resources in a manner consistent with their origi-
nal site (Rittenhouse et al. 2008), sometimes with negative con-
sequences to their performance in the new environment
with familiar hibernation sites may also account for the trend
of translocated individuals maintaining surface activity later in
the season (Fig. 1). Snakes in cold climates often maintain
strong fidelity to specific overwintering areas (Prior, Blouin-
Demers & Weatherhead 2001; Harvey & Weatherhead 2006),
and may travel long-distances in an attempt to return if dis-
placed (Brown & Parker 1976). The long-distance movements,
large areas traversed and off-site explorations were likely to be
a result of translocated snakes searching for cues matching
resource selection templates developed previously.

It is also possible that introduced snakes were less healthy as
a result of the translocation process or the conditions they
experienced prior to release. For instance, parasites can impact
growth rates and body condition of snakes (Madsen, Ujvari &
Olsson 2005), and snakes translocated from another site or
raised in captivity may have been differentially exposed to par-
asites and other pathogens. At the time of release, however,
resident snakes actually had the lowest BCIs, and we observed
no overt manifestations of disease or parasitism in any individ-
uals. We later discovered the nematode Eustrongyldes ignotus
in some snakes in our captive colony, but this parasite was
probably introduced via wild-caught prey from the release site
which was fed to captives. This nematode is known to occur in
the region of our study (Friend et al. 1999).

MANAGEMENT IMPLICATIONS

We view the causes responsible for the poor performance
of head-started water snakes as presenting more problems for
reintroduction programmes than for those translocated
directly from the wild. Although translocated snakes had low
survivorship, they demonstrated an ability to more effectively
use resources at the release site. The number of translocated
animals could be adjusted to meet desired survivorship and
site-retention goals, but the release of numerous individuals
can risk compromising the viability of source populations. In
such cases, captive colonies could feasibly generate stock for
reintroductions, but our captive-reared snakes lacked the
behavioural competence for survival in the wild, and would
thus be ill-suited as population founders in a reintroduction
programme regardless of the number released.

That an animal’s prior experience appears to factor
importantly in determining their behaviour and ultimate
survival during the phase of early establishment at an unfami-
lar site provides a potentially useful framework for improving
reintroduction efforts (Davis & Stamps 2004; Stamps & Swais-
good 2007). Reintroductions are likely to be most successful
when habitats (and associated resources and conditions) are
matched between source and release sites (Rittenhouse et al.
2008). When such matches are not possible, the performance
and site fidelity of translocated animals may be improved by
temporarily confining them in enclosures that allow new
associations to be made while avoiding the dangers of

exploratory wanderings (Bright & Morris 1994; Tuberville et al. 2005). Such efforts could include identifying or creating suitable overwintering refuges for snakes (Kissner & Weatherhead 2005), as the consequences of not finding a suitable overwintering site can be particularly catastrophic (Macmillan 1995). Head-starting programmes using captive animals may also be improved by providing housing in environmentally enriched conditions that match release sites as closely as possible. Reintroduction programmes drawing from captive stock should be aware of the difference between outputs of animals and conservation outputs, as facilities and practices designed strictly for animal husbandry will be different to those designed to produce animals best prepared for life in the wild—the latter being the preferred strategy for reintroduction, but also the most costly (Miller et al. 1999; Brown & Day 2002; Alberts 2007).

A clear limitation in this study was the small sample sizes, especially with regards to the details of how different demographic groups may respond to reintroduction. Given the typically strong influence of sex, size, age and reproductive status on their performance at novel sites. Instead of closing the door on animal reintroductions, is it our hope that this research will open additional avenues for experimental approaches to reintroductions designed to be of utility to conservation professionals.

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