The effect of translocation on movement behaviour—A test of the assumptions of behavioural studies

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A R T I C L E  I N F O
Article history:
Received 9 December 2008
Received in revised form 3 March 2009
Accepted 4 March 2009

Keywords:
Capture-mark-recapture
Handling effect
Oedipoda caerulescens
Orthoptera

A B S T R A C T
Animal movement behaviour is intensively investigated with capture-mark-recapture studies. For the analysis of such experiments, the influence of marking technique, handling and translocation of marked animals on movement pattern is of crucial importance since it may mask or overrule the effects of the main research question. Here we present a capture-mark-recapture experiment on the movement behaviour of the blue-winged grasshopper Oedipoda caerulescens. We analyzed the influence of translocation of individuals from familiar to unfamiliar sites. Our study clearly demonstrates a significant influence of translocation to unfamiliar sites on the movement behaviour of O. caerulescens. Translocated individuals moved longer distances, showed smaller daily turning angles, and thus movements were more directed than those of resident individuals. The effect of translocation on daily moved distances was most pronounced on the first day of the experiment. We thus conclude that at least for the first day after translocation, movement behaviour is significantly influenced by translocation itself. Data ignoring this influence will be unsuitable for the prediction of dispersal behaviour, habitat detection capability or habitat preference.

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1. Introduction

Dispersal plays a crucial role in the ecology and evolution of species and the persistence of metapopulations (Rouquette and Thompson, 2007; Wu et al., 2000; Schtickzelle et al., 2007; Dieckmann et al., 1999; Poethke et al., 2003; Hövestadt and Poethke, 2006). It influences the dynamics and persistence of populations, the distribution and abundance of species, community structure, the level of gene flow between populations, local adaptation, speciation and determine how organisms respond to fragmentation of landscape and climate change (Bullock et al., 2002; Clobert et al., 2004; Dieckmann et al., 1999; Hanski, 1999). As fragmentation of landscapes is increasing and the number of species is continuously declining, a thorough understanding of the processes governing dispersal is becoming more and more important and may be essential in developing effective conservation strategies (Baguette et al., 2000; Caughley, 1994; Diekkoetter et al., 2007).

In the context of animal dispersal, movement behaviour has been frequently investigated with capture-mark-recapture studies (Berggren, 2004; Hein et al., 2003; Baguette and Neve, 1994; Hill et al., 1996; Kindvall, 1999; Ricketts, 2001). Conclusions drawn from these studies crucially depend on the assumption that the marking technique and the translocation of animals from their familiar habitat patch to unfamiliar sites have no (or at most a negligible) influence on the behaviour of these individuals.

The impact of different marking methods on the physiology and behaviour of marked animals has been investigated in many studies. Most of them showed no significant effect on behaviour, body weight and growth, flight ability, mating propensity and fecundity, mortality or predation risk due to markings (Cooley et al., 1998; Ambrose, 1972; Binninger, 2000; Lindner and Fuelling, 2002; Evans and Gleeson, 1998; Bates and Sadler, 2004; Henry and Jarne, 2007; Kobayashi and Kikuchi, 2004). In contrast, some studies revealed a negative influence of the marking on the activity, body weight, survival and recapture rates of marked animals (Gall, 1984; Korn, 1987; Pavone and Boonstra, 1985; Fairley, 1982; Wood and Slade, 1990).

In many capture-mark-recapture studies, animals are captured at one site, their familiar “home” site, and transferred to other unfamiliar sites to investigate their behaviour. Unfamiliar sites may comprise suitable habitat (Kindvall, 1999; Berggren, 2004, 2005) or different types of unsuitable sites (matrix) (Hein et al., 2003; Kindvall, 1999), where animal behaviour is studied, e.g. to predict how fast or well this area can be crossed to reach suitable habitat. In such a case, it is very important that translocation itself does not influence movement behaviour since it is impossible to separate other effects, for example type of matrix, from the effect of...
translocation. Nevertheless, to our knowledge, there is no study focusing on the impact of translocation itself although there is some evidence that transferring animals to suitable but unfamiliar sites has an effect on the movement behaviour of translocated individuals. Jacquot and Solomon (1997) investigated the effect of site familiarity on movement pattern of male voles. In this experiment, individuals released in unfamiliar outdoor enclosures moved farther than their conspecifics released in familiar enclosures. However, not only translocation but also social interactions between translocated and resident males could have influenced the movement behaviour of translocated individuals. In addition, bird reintroduction studies of endangered species for conservation purpose revealed that for birds extensive and rapid movement seems to be typical after their release in unfamiliar habitat, even in normally sedentary species (Clarke and Schedvin, 1997; Armstrong et al., 1999). There are also experiments on homing behaviour after artificial translocation to unfamiliar sites with birds, fishes and snails which show that animals react on translocation (Tomiyama, 1992; Armstrong and Herbert, 1997; Belanger and Rodriguez, 2001). However, since translocation was not the main focus of these studies, the effects on individual behaviour could not be verified. With no control group the impact of translocation cannot be distinguished from other potentially confounding factors that could have influenced behaviour. Here we present a capture-mark-recapture study on the effect of translocation on movement behaviour of the blue-winged grasshopper O. caerulescens in coastal grey dunes. We chose a grasshoppers species because grasshoppers are often used as bioindicators and capture-mark-recapture experiments are easily conducted with grasshoppers (Andersen et al., 2001). In our study, we investigated individuals of O. caerulescens on two sites simultaneously to exclude an influence of the study site, where individuals were released or the population where individuals originated from.

2. Materials and methods

2.1. Study species

The blue-winged grasshopper Oedipoda caerulescens (LINNAEUS 1758; Orthoptera: Acrididae) is a thermo- and xerophilic grasshopper species of medium to large size (body length: 15–30 mm) (Detzel, 1998). O. caerulescens inhabits stony calcareous meadows with sparse vegetation, quarries and sand pits and can also be found in dry heathlands, spoil heaps and railroad yards (Schlumprecht and Waaber, 2003). This species is described as moderately sedentary although some individuals can move over long distances up to 800 m (Maes et al., 2006; Hein et al., 2005). Individuals usually move on the ground but fly a few meters (3–6 m) if disturbed. Long distance flights are seldom observed (Detzel, 1998).

2.2. Field work

The study was carried out in the Westhoek Nature Reserve (De Panne, Belgium; 51 °3′N–51 °05′N, 2 °34′E). For our experiments, we chose two study sites of typical grey dunes, characterised by open sand, moss and herbaceous plants. Distance between both sites was about 825 m. On each site, we caught 14 females and 14 males of O. caerulescens and marked their exact position where an individual was found with a numbered stick. This position is assumed to represent the preferred microhabitat of each individual. Grasshoppers were individually marked with numbered reflective tape, fixed on the femur of one hind leg (Heller and von Helversen, 1990). Until all insects were released in the late evening next to a numbered stick, we kept them in numbered plastic vials in a cooling box to reduce potential handling trauma (Stettmer, 1996).

To investigate movement behaviour in the familiar habitat patch half of the individuals (7 females, 7 males) captured on one site were randomly chosen and released exactly at the position where they were found (resident individuals). The second half of grasshoppers were transferred to the respective other site and released to test their movement behaviour in unfamiliar suitable habitat (translocated individuals). Thus, half of the caught individuals from one patch were replaced by individuals of same sex from the other patch thereby keeping density constant in both patches. As a control for a potentially different microhabitat choice of females and males, we released females only at positions where females were caught and males only at positions where males were caught.

We determined the position of each (re-sighted) individual in the following four nights. Thereby daily moved distances, turning angles and net displacement after each day were recorded. The first recapture of individuals was 24 h after release. We chose an observation interval of 24 h.

2.3. Re-sight rates

Re-sight rates allow an estimation of mortality (or emigration) rates, detection error and the quality of the marking method. We used re-sight rates of individuals as well as findings of lost reflective tape to compare our two study sites with respect to these factors. Tape could either be lost accidentally or be left by predators feeding on grasshoppers. Individuals that we could not find on one day, but that were re-sighted on one of the following days were probably overlooked and allow an estimation of the detection error during the experiment. Individuals that we never re-sighted until the end of the observation period were assumed either to be dead or to have emigrated.

2.4. Statistical analyses

Analysis of data was complicated by the fact that not all individuals were found continuously in the four observation nights resulting in incomplete data sets on movement distances and turning angles. For statistical analysis we chose only data resulting from measurements during two consecutive nights, even if the record was previously interrupted (see also Hein et al., 2003). Linear mixed-effects models were applied to analyse the effect of sex, translocation, release site and capture site on movement behaviour of O. caerulescens. As we caught individuals at several consecutive days, ‘individual’ and ‘day’ were used as random effects in all models. Starting from a full model (all main factors and all interaction terms), model selection was conducted by stepwise backward elimination of not significant interaction terms with p-values above 0.15. We did not remove main factors, even if they were non-significant. Sequential type III sums of squares were used in all F-tests to analyze whether a significant proportion of variance in movement parameters could be explained by sex, translocation, release site or capture site. Parameter estimates were obtained using the restricted maximum log-likelihood (REML) method. We used log-likelihood (ML) fits for model comparison with Akaike’s Information Criterion as model selection criteria. For statistical analyses, distance data were box–cox transformed and angle data were Johnson transformed. To compare daily moved distances and turning angles between resident and translocated individuals for each recapture day, we used Mann–Whitney U-tests for two independent samples. All analyses were conducted with the statistics software packages R 2.6.2 (r-project.org) and SAS 9.1.

3. Results

3.1. Re-sight rates

The loss of individuals (mortality and/or emigration) was highest for translocated animals on site one (>60% at last recapture day).
Table 1  
Effects of sex, translocation and release site on box–cox transformed daily moved distances of all individuals and males of *O. caerulescens*. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), *F* and *p*-values of mean effects as derived from a linear mixed-effects model after model selection are given.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Estimate (b)</th>
<th>SE</th>
<th>Den. d.f.</th>
<th>F-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily moved distances of all individuals on both sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>0.16</td>
<td>0.05</td>
<td>37.8</td>
<td>47.33</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Translocation</td>
<td>−0.08</td>
<td>0.04</td>
<td>34.5</td>
<td>4.96</td>
<td>0.03</td>
</tr>
<tr>
<td>Release Site</td>
<td>−0.09</td>
<td>0.05</td>
<td>38.3</td>
<td>0.21</td>
<td>0.65</td>
</tr>
<tr>
<td>Sex × Release Site</td>
<td>0.22</td>
<td>0.08</td>
<td>37.5</td>
<td>7.94</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Daily moved distances of males on both sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Translocation</td>
<td>−0.17</td>
<td>0.10</td>
<td>16.9</td>
<td>2.74</td>
<td>0.12</td>
</tr>
<tr>
<td>Release Site</td>
<td>0.22</td>
<td>0.11</td>
<td>18.8</td>
<td>4.22</td>
<td>0.04</td>
</tr>
</tbody>
</table>

In general, the proportion of lost individuals was higher for animals released on site one than for those released on site two, irrespective of whether they were translocated or not. Corresponding to this finding, the proportion of not continuously re-sighted animals was higher for study site one than for site two. Re-sight rates were highest for the resident individuals on study site two where day-to-day re-sight rates were >80% during the whole experiment. For both study sites, proportion of not continuously re-sighted animals was higher for translocated individuals than for resident ones.

3.2. Movement behaviour

Our results clearly show that translocation had an impact on the behaviour of individuals. Compared to animals which were released in their familiar habitat patch, translocated individuals moved longer distances per day (Table 1, Fig. 1) and showed greater net displacement (Table 2, Fig. 1). Besides translocation, the sex of an individual significantly influenced daily moved distances and net displacement with males moving longer distances than females (Tables 1 and 2). In addition, interaction between sex and release site had a significant influence on daily distances (Table 1) and net displacement (Table 2) too. The effect of translocation on daily moved distances was most pronounced at day one and was not significant on the following days (Mann–Whitney *U*-test, *p* < 0.05; Fig. 2). For daily turning angles, translocation had a tendentious effect (Table 3), with translocated animals showing smaller turning angles than resident ones. The sex of an individual had no effect but interaction between translocation and release site significantly influenced daily turning angles (Table 3). However, no significant differences of daily turning angles between translocated and resident individuals on single days could be found.

Separate analyses for each sex revealed that the site where an individual was released had an influence on daily moved distances (Table 1, Fig. 3) and net displacement (Table 2, Fig. 3) for males but not for females. Males moved significantly longer distances on study site one than on study site two, irrespective of their origin. Furthermore, the interaction effect of translocation and release site on daily turning angles (see above) was significant for males (Table 3). In contrast to males, this effect was not significant for females.
Table 3  
Effects of sex, translocation, release site and capture site (population of origin) on Johnson transformed daily turning angles of all individuals and males of *O. caerulescens*. Estimates, standard errors of estimates (SE), denominator degrees of freedom (Den. d.f.), $F$ and $p$-values of mean effects as derived from a linear mixed-effects model after model selection are given.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Estimate ($b$)</th>
<th>SE</th>
<th>Den. d.f.</th>
<th>$F$-value</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily turning angles of all individuals on both sites</td>
<td></td>
<td>0.15</td>
<td>0.21</td>
<td>86</td>
<td>0.48</td>
</tr>
<tr>
<td>Sex</td>
<td></td>
<td>0.18</td>
<td>0.26</td>
<td>86</td>
<td>2.83</td>
</tr>
<tr>
<td>Translocation</td>
<td></td>
<td>0.72</td>
<td>0.34</td>
<td>86</td>
<td>0.44</td>
</tr>
<tr>
<td>Release Site</td>
<td></td>
<td>1.13</td>
<td>0.46</td>
<td>86</td>
<td>6.12</td>
</tr>
<tr>
<td>Translocation × Release Site</td>
<td></td>
<td>0.28</td>
<td>0.37</td>
<td>42</td>
<td>2.45</td>
</tr>
<tr>
<td>Daily turning angles of males on both sites</td>
<td></td>
<td>0.83</td>
<td>0.54</td>
<td>42</td>
<td>0.09</td>
</tr>
<tr>
<td>Translocation</td>
<td></td>
<td>1.64</td>
<td>0.69</td>
<td>42</td>
<td>5.58</td>
</tr>
<tr>
<td>Release Site</td>
<td></td>
<td>0.72</td>
<td>0.34</td>
<td>86</td>
<td>0.44</td>
</tr>
<tr>
<td>Translocation × Release Site</td>
<td></td>
<td>1.13</td>
<td>0.46</td>
<td>86</td>
<td>6.12</td>
</tr>
<tr>
<td>Daily turning angles of all individuals released on site one</td>
<td></td>
<td>0.60</td>
<td>0.39</td>
<td>10.8</td>
<td>2.44</td>
</tr>
<tr>
<td>Sex</td>
<td></td>
<td>0.83</td>
<td>0.38</td>
<td>10.9</td>
<td>4.69</td>
</tr>
<tr>
<td>Translocation</td>
<td></td>
<td>1.36</td>
<td>0.46</td>
<td>11</td>
<td>8.65</td>
</tr>
<tr>
<td>Daily turning angles of males released on site one</td>
<td></td>
<td>0.92</td>
<td>0.41</td>
<td>26</td>
<td>4.97</td>
</tr>
<tr>
<td>Capture Site</td>
<td></td>
<td>0.52</td>
<td>0.41</td>
<td>26</td>
<td>4.97</td>
</tr>
</tbody>
</table>

Separate analyses for each release site showed that for study site one translocated individuals showed smaller daily turning angles and thus moved more directed than resident ones (Table 3). This effect of translocation on daily turning angles was significant for males (Table 3, Fig. 4) whereas it was not for females (Fig. 4) and not for individuals released on experimental area two. In addition to this finding, resident males captured and released on study site one showed larger turning angles than resident males on site two (Table 3, Fig. 5). For females, such an effect could not be detected.

Fig. 3. Comparison of daily moved distances (white) and net displacement (grey) between males released on study site one and two.

Fig. 4. Comparison of daily turning angles between resident and translocated males (white) and females (shaded) of *O. caerulescens* released on study site one.

Fig. 5. Comparison of daily turning angles between resident males of *O. caerulescens* captured on study site one and two.

4. Discussion

4.1. Movement behaviour

Our experiment clearly demonstrates an influence of translocation on movement behaviour of individuals in capture-mark-recapture studies. Translocated individuals of *O. caerulescens* moved...
longer distances irrespective of site, showed smaller daily turning angles on site one and thus moved more directed than resident individuals. The latter showed rather routine movements, which are characterized by short distances and large turning angles and which animals usually show when they are moving in their familiar habitat (Van Dyck and Baguette, 2005).

Effect of translocation on daily moved distances was only significant on the first day after translocation. The most likely explanation might be that translocated individuals showed a change in movement behaviour after translocation and then switched to routine movements after habituating to the unfamiliar surrounding. The effect of translocation is limited to a certain time period after release. Such a temporal effect has also been shown for the influence of marking on butterflies in a capture-mark-recapture experiment, where the handling of animals disrupted flight activity solely at the day when individuals were captured for the first time and marked (Gall, 1984). In addition, bad weather conditions after the first recapture could have led to a reduced activity of test individuals as *O. caerulescens* is a thermophilic species with low activity at low temperatures (Detzel, 1998; Walters et al., 2006). However, daily maximum temperature was highest at the last day of experiment and nonetheless translocated animals moved shorter distances compared to the first day of experiment. This indicates that weather conditions alone cannot explain the attenuation of translocation effect after the first day.

Daily distances and net displacement for males released on study site one were longer than for those on site two. This finding could be explained by the fact, that site one is twice as large as site two and males do not encounter boundaries that often. In small habitat patches, individuals encounter patch boundaries more frequently than in large ones while avoiding to cross them and moving back to the inner part of the habitat patch (Ross et al., 2005; Schtickzelle and Baguette, 2003; Ries and Debinski, 2001). On large sites, individuals can move longer distances without reaching the boundary. Thus, our finding is in good accordance with previous studies which have shown that movement or dispersal distances of insects and vertebrates increases with study area size (Franzén and Nilson, 2007; Schneider, 2003; Koenig et al., 1996). In our experiment, the effect of study site size was not significant for females presumably because they are in general less active than males (Maes et al., 2006).

On study site one, translocated males moved more directed than resident ones whereas on site two this effect was not significant. In addition, resident males captured and released on study site one showed larger turning angles than resident males on site two. Thus, local conditions of sites where individuals were released or originated from also influence individual behaviour and may enhance or attenuate the effect of translocation. According to local conditions, reaction of individuals on translocation can vary and therefore the impact of translocation is difficult to predict.

Effect of translocation was most pronounced on the first day of the experiment, but may persist for longer. The exact duration of this translocation effect is difficult to determine and may depend on species and weather conditions. Although our results are restricted to *O. caerulescens*, we expect that similar effects of translocation could also occur in other arthropods. On average, daily moved distances of translocated individuals were about 50% longer (9.14 m ± 12.25 m) than of resident individuals (6.17 m ± 8.87 m) because they have been transferred to an unfamiliar habitat patch. Depending on experiment duration, this leads to considerable differences in net displacement between translocated and resident individuals. Therefore, extrapolation on dispersal behaviour based on movement data derived from capture-mark-recapture experiments is, strictly speaking, only valid if individuals are released at the same position (at least on the same site) where they have been caught. In addition, for the comparison of movement patterns in different habitat types, a control experiment observing translocated individuals in a new suitable habitat is required. In summary, our results clearly point out that translocation effects should not be disregarded in future studies on arthropod movement, respectively dispersal.

4.2. Re-sight rates

The analysis of re-sight data shows that loss of individuals was higher for study site one than for site two. This is probably not due to differences in predation risk or food availability. In our experimental design we tried to choose areas of similar vegetation composition, vegetation structure and amount of open soil thus we assume no differences in food availability and predation risk between the two study sites. For both sites, proportion of not continuously re-sighted animals was higher for translocated individuals than for resident ones. Translocation may lead to a higher propensity of the translocated animals to leave an unfamiliar habitat patch or to move further away from the release point at least. In contrast, resident individuals may tend to stay where they are in their familiar habitat patch and thus are easier to find which leads to higher re-sight rates. Translocated individuals may also experience an increased predation risk because they are released in an unknown surrounding in which they take longer to reach cover and may show atypical behaviour (Ambrose, 1972; Metzgar, 1967; Jacquot and Solomon, 1997). In addition, increased movement, maybe due to orientation behaviour in the new surrounding, of translocated individuals may lead to an increased predation risk compared to resident individuals (Yoder et al., 2004).

Acknowledgements

Koen De Smet (Head of the Nature Department of the Flemish Nature Conservation Ministry) granted us permission to study the legally protected *O. caerulescens* (licence number AMINAL/NAT/DL.832.172/2275). We thank Brecht Decausmaecker for conducting the fieldwork. Dries Bonte is a postdoctoral fellow of the Fund for Scientific Research – Flanders (FWO). Ina Heidinger was funded by the “Deutsche Bundesstiftung Umwelt” (DBU).

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