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Restoration and Rescue in an Age of Extinction: Advances in Arthropod Reintroduction (and Translocation)

Radio telemetry reveals extensive dispersal capabilities of reintroduced Great Capricorn beetles (*Cerambyx cerdo*) in oak habitats at their northern range limit

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Abstract

1. Amid accelerating global biodiversity loss, reintroducing and translocating endangered species have become pivotal conservation strategies. This study used radio telemetry to investigate the dispersal and movement patterns of the reintroduced Great Capricorn Beetle *Cerambyx cerdo* (Coleoptera: Cerambycidae) L. within Tromtö Nature Reserve, Sweden.
2. We tracked 50 beetles (29 females, 21 males) from 17 June 2022 to 17 July 2022, quantified their movements within the landscape and recorded the distances moved across oak-rich areas at the northern edge of the species' range.
3. Female beetles were significantly larger and heavier than males, with longer antennae. The beetles were relocated an average of 9.5 times. Total movement distances ranged from 2.8 to 822.2 m, with no significant association of movement distance or movement speed with sex, body size or mating status.
4. We conclude that *C. cerdo* can reach oaks several hundred meters away and that dispersal distances were not associated with sex, body size or mating status. We recommend future studies employing more advanced telemetry techniques to refine estimates of long-distance dispersal and habitat use.

KEYWORDS
conservation biology, endangered species, insect translocation, movement ecology, oak habitat conservation, reintroduction strategies

INTRODUCTION

Global biodiversity is declining at an alarming rate, with insects experiencing significant losses due to habitat destruction, fragmentation and climate change (Sánchez-Bayo & Wyckhuys, 2021; Wagner et al., 2021). Saproxylic insects—species dependent on dead or decaying wood—are particularly vulnerable because of the reduction in ancient trees and coarse woody debris resulting from modern forestry practices and land-use changes (Calix et al., 2018; Müller et al., 2014; Seibold & Thorn, 2018). The Great Capricorn Beetle *Cerambyx cerdo* L., a large longhorn beetle associated with 'veteran' oak trees—older trees often featuring hollow trunks or decaying wood that support diverse saproxylic communities—exemplifies these challenges and is considered a priority European conservation species (Buse et al., 2007; Eide et al., 2020; Mannu et al., 2021).

At its northernmost range in Sweden, *C. cerdo* depends on specific ancient oak tree habitats that provide suitable microclimates (Albert et al., 2012). Insect populations at species range margins often experience increased population fluctuations and higher extinction risks than populations at the core of the species distribution (Thomas et al., 1994). Such populations at range margins are in urgent need of conservation actions. However, when temperatures become warmer due to climate change, *C. cerdo* might expand northwards (Pélissié et al., 2022; Sunde et al., 2023; Wilson & Fox, 2021). Thus, it is critical to study movement patterns and habitat use of *C. cerdo* at its northern range limit where habitats are becoming increasingly fragmented and isolated (Eliasson & Nilsson, 2002). Habitat fragmentation reduces available habitat and affects the connectivity between habitat patches, influencing species' dispersal and colonisation abilities (Fahrig, 2017). Dispersal is a critical life-history trait determining a species' capacity to track environmental changes, colonise new habitats and maintain genetic diversity (Bowler & Benton, 2005). A previous study shows that body size influences dispersal capabilities that are greater in larger beetles (Terlau et al., 2023), and theory posits there might be differences in dispersal between sexes and according to mating status (Li & Kokko, 2019; Saveer et al., 2021).

Our study included both mated and unmated females to examine how mating status influences dispersal, often overlooked in insect studies. Mated females may exhibit different movement patterns due to reproductive demands, while unmated females prioritise mate-seeking behaviour (Saveer et al., 2021). Species with low dispersal abilities are particularly susceptible to the adverse effects of habitat fragmentation (Hanski, 2011). For such species, conservation efforts must focus on maintaining habitat connectivity and ensuring suitable habitats are available within dispersal distances (Moilanen & Hanski, 2001; Ranius & Kindvall, 2006). Understanding the dispersal behaviour of *C. cerdo* is essential for developing effective conservation strategies, especially at the edges of its distribution where populations may be more isolated and vulnerable (Platek et al., 2019).

Previous studies on the dispersal of *C. cerdo* have yielded mixed results, with some studies suggesting limited dispersal abilities and others indicating the potential for longer-range movements (Buse et al., 2007; Drag & Cizek, 2018). Studies often rely on mark-recapture methods or indirect measures, which may not accurately assess the true dispersal capabilities of the study species due to detection biases and limited detection ranges (Franzen & Nilsson, 2007; Nathan et al., 2012).

While a growing number of studies explicitly link movement ecology to conservation goals, with 60% of available research being incorporated into species status assessments, significant knowledge gaps persist for many at-risk taxa, underscoring the need for broader application of movement research in conservation planning (Fraser et al., 2018). For reintroduced species, some insects have been monitored using traditional marking methods, such as the American burying beetle (*Nicrophorus americanus*) (Amaral et al., 1997) and the Large Blue butterfly (*Phengaris arion*) in the UK (Simcox et al., 2024). However, most studies of reintroduction movement patterns focus on larger species, such as mammals (Berger-Tal & Saltz, 2014). Radio telemetry has emerged as a powerful tool for studying the movement ecology of threatened insects, offering insights into dispersal behaviour and habitat use that are difficult to obtain through other methods (Růžičková & Elek, 2023). This approach has been successfully applied to saproxylic beetles, including *Osmoderma eremita* (Hedin & Ranius, 2002), *Lucanus cervus* (Rink & Sinsch, 2007) and *Rosalia alpina* (Drag et al., 2011), revealing critical aspects of their spatial ecology.

In this study, we employ radio telemetry to investigate the movement ecology of the reintroduced *C. cerdo* beetle at its northernmost range margin in Sweden's Tromtö Nature Reserve. By tracking the movements of individual beetles equipped with radio transmitters, we aim to:

1. Provide information about ongoing reintroduction activities associated with *C. cerdo* in Sweden.
2. Quantify movement distances of *C. cerdo* and explore associations with sex, body size and mating status.
3. Provide insights to inform conservation and reintroduction strategies for *C. cerdo* and other threatened saproxylic insects.

MATERIALS AND METHODS

Rearing and conservation programme at Nordens Ark

To address the urgent conservation need of the critically endangered *C. cerdo* in Sweden (Eide et al., 2020), Nordens Ark initiated a pioneering breeding program in 2012, in collaboration with the County Administrative Boards of Kalmar and Blekinge, as part of Sweden's national species conservation action plan. The breeding stock was sourced from Halltorps Hage (coordinates 56.81 N, 16.59 E), the last natural stronghold of *C. cerdo* in Sweden, to minimise the impact on the wild population. Larvae were reared in controlled conditions within Petri dishes containing a custom-formulated substrate made from oak (*Quercus* spp.) shavings, providing optimal nutritional and environmental conditions. The larval stage lasted approximately two years, resembling the species' natural development cycle. During this time, larvae were monitored regularly for growth and development. Upon reaching pupation, individuals were closely observed during their transition to adulthood, typically in late summer. After emergence, adult beetles are overwintered in specialised refrigeration units set to temperatures that mimic natural winter conditions to ensure reproductive maturity. This overwintering process is critical for synchronising the reproductive cycle with natural environmental cues. Since 2017, Nordens Ark has released between 150 and 300 beetles annually into carefully selected protected areas in Sweden, including Björnö (coordinates 56.77 N, 16.36 E) and Tromtö (coordinates 56.16 N, 15.49 E), which provide habitats conducive to *C. cerdo* survival and reproduction. The selection of release sites was based on detailed habitat assessments, focusing on the availability of veteran oak trees and suitable microhabitats. Post-release monitoring is ongoing to assess the emergence of reintroduced *C. cerdo* from pupae and the investigation of habitat utilisation. In captivity one to two days before release, 19 of the female beetles were mated, while 10 remained unmated.

Study area

This study was conducted in Tromtö Nature Reserve, in Karlskrona municipality, Sweden (Figure 1a,b). The reserve is characterised by a rich diversity of habitats, most notably featuring ancient and hollow oak (*Quercus* spp.) (Figure 1c), which are critical to the lifecycle of *C. cerdo* (Figure 1c,d). The area is managed through a traditional grazing regime involving sheep and cattle, which helps maintain the open landscape and the health of veteran trees. A telemetry field study was conducted over five weeks, from 16 June to 17 July 2022.

Radio telemetry methods

The *C. cerdo* beetles used in this study originated from the Nordens Ark breeding program. We equipped 50 individuals (29 females,

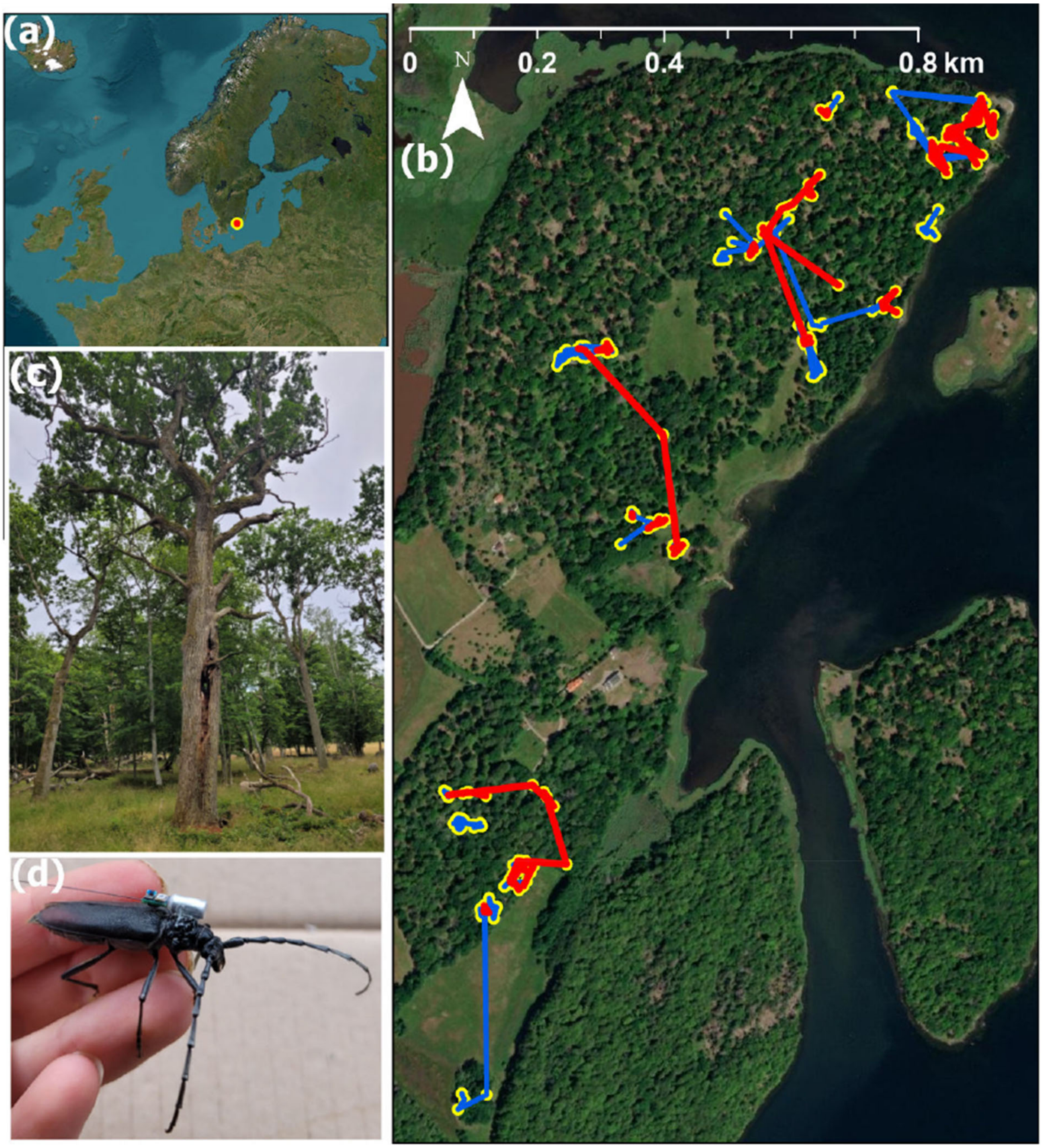

FIGURE 1 (a) Maps showing the geographic location of the study area in southern Sweden, with the approximate location of Tromtö marked with a dot. (b) A detailed aerial view of the studied area with individual beetle movement paths is overlaid. Yellow dots represent beetle observation points, and lines indicate movement paths. Movement paths for males are shown in red, and those for females are shown in blue. (c) Photograph of a mature oak (*Quercus robur*), a suitable habitat for *Cerambyx cerdo*, located within the Tromtö Nature Reserve. (d) The Great Capricorn Beetle (*C. cerdo*) is equipped with a radio telemetry tag.

21 males) with NanoPin transmitters (model NTP-1, Lotek Wireless Inc., Newmarket, Ontario, Canada). Each transmitter weighed 0.13 g with 11 mm length and 5 mm diameter dimensions, featuring a 12 cm flexible antenna (Figure 1d). Transmitters were activated using a NanoTag activator (model NANOTAG IR ACT) and had an operational battery life of up to 30 days. Prior to release, we measured each beetle's body weight to the nearest 0.01 g using a Kern EMB series precision balance and recorded body length, antenna length (to nearest mm) and pronotum width (to nearest 0.1 mm) using digital callipers. Beetles were equipped with radio transmitters on their pronotum using cyanoacrylate glue (Super Loctite Super Glue Original), with the transmitter antenna extending along the abdomen to minimise interference with movement. Beetles were released in five batches between 17 and 27 June 2022 (18 on 17 June, 16 on 20 June, 13 on 22 June, 4 on 26 June and 2 on 27 June) onto 22 suitable ancient oak trees (*Quercus* spp.) within the Tromtö Nature Reserve. Release trees were selected based on trunk size, sun exposure and overall tree health.

We conducted daily tracking using a Biotracker receiver (model BIOTRACKER8 146–154 MHz) with a whip antenna (model SLA/FT-2). One person systematically searched the Tromtö Nature Reserve and adjacent areas up to 3 km away. Each beetle was then searched for once per day during these searches. Beetle locations and activity were documented using Field Maps (Esri), which automatically recorded time, user and coordinates for each observation. Tracking continued until 17 July 2022.

Statistical analyses

All statistical analyses were conducted using R version 4.4.1 (R Core Team, 2024). Morphological differences between sexes were assessed using independent two-sample *t* tests, with Welch's correction applied when variances were unequal (as determined by Levene's test). Similarly, we used *t* tests to statistically evaluate whether the total distance moved, movement speed and the number of relocated beetles differed between sexes and mating status. We used linear models (lm function) to investigate the relationship between total distance moved, body length and sex. Preliminary analyses revealed strong correlations between morphological measurements (body length, pronotum width and weight were all correlated with $r > 0.70$). To avoid multicollinearity in our analyses, we selected body weight as our primary morphological predictor, as it provided the most direct measure of size. Individual movement was measured as the cumulative Euclidean distance between successive tracking points, representing the total distance traversed by each beetle. Values were natural log-transformed prior to analysis to address non-normality in the distribution of movement distances. This transformation was validated through a Shapiro–Wilk test ($W = 0.97$, $p = 0.186$ for log-transformed data). To evaluate if movement distance relates to body length and sex combined in one model, we constructed a linear model that included the interaction between body length and sex to examine their effects on movement distance. The interaction was not significant and was consequently removed.

RESULTS

Beetle characteristics

Female beetles were significantly heavier than males (1.53 ± 0.03 g vs. 1.27 ± 0.03 g, mean ± SE, respectively; Welch's *t* test: $t(49.44) = 6.75$, $p < 0.001$) (Figure 2a), and had a significantly longer body length than males (38.06 ± 0.24 mm vs. 36.92 ± 0.28 mm, mean ± SE, respectively; Welch's *t* test: $t(45.48) = 3.10$, $p = 0.003$). Females also tended to have a larger pronotum width than males (8.54 ± 0.06 mm vs. 8.33 ± 0.09 mm, mean ± SE, respectively; Welch's *t* test: $t(36.35) = 1.93$, $p = 0.061$). Male beetles had significantly longer antennae than females (58.07 ± 0.71 mm vs. 36.46 ± 0.25 mm, mean ± SE, respectively; Welch's *t* test: $t(25.10) = -28.62$, $p < 0.001$).

Movement patterns

The mean total distance moved was 153 ± 23.9 m (mean ± SE) (Figure 2b). Males moved an average total distance of 155 ± 38.8 m, while females moved 152 ± 30.8 m (mean ± SE). The mean movement speed, calculated as the total distance moved divided by the number of tracking days, was 9.6 ± 2.1 m/day for males and 8.6 ± 1.4 m/day for females (mean ± SE). On average, beetles were tracked for 16.2 days, with males tracked for 14.9 ± 2.1 days and females for 17.2 ± 1.4 days. Welch's *t* tests showed no significant differences between males and females in total distance moved ($t(41.36) = -0.04$, $p = 0.97$) or movement speed ($t(36.87) = -0.40$, $p = 0.70$) (Figure 2c,d). In the model, combining body length and sex neither of them significantly predicts movement distance ($F_{1,47} = 1.65$, $p = 0.21$), sex ($F_{1,47} = 0.29$, $p = 0.59$) (Figure 3).

Among the 29 tracked females, 19 were mated and 10 were unmated. The mean total distance moved by mated females was 163 ± 42.5 m (mean ± SE), compared to 133 ± 40.1 m for unmated females. The mean movement speed for mated females was 9.33 ± 1.72 m/day, while unmated females averaged 7.27 ± 2.65 m/day. Statistical analyses using Welch's *t* tests revealed no significant difference in total distance moved between mated and unmated females ($t(24.90) = 0.52$, $p = 0.61$). Similarly, movement speed did not significantly differ between the two groups ($t(16.71) = 0.65$, $p = 0.52$).

Notably, 23 individuals moved >100 m during the study period. The farthest movement recorded was by a female beetle, moving 822 m (Figure 1b), and the corresponding distance for males was 601 m. The average number of days between the first and last day of relocation was 15.3 days (min = 0, max = 30). There was no significant difference in the number of relocated beetles between female and male beetles (10.14 ± 0.79 vs. 9.57 ± 1.18, mean ± SE, respectively; Welch's *t* test: $t(36.54) = 0.40$, $p = 0.69$). The multiple linear models revealed no significant effects of body length ($F_{1,47} = 0.19$,

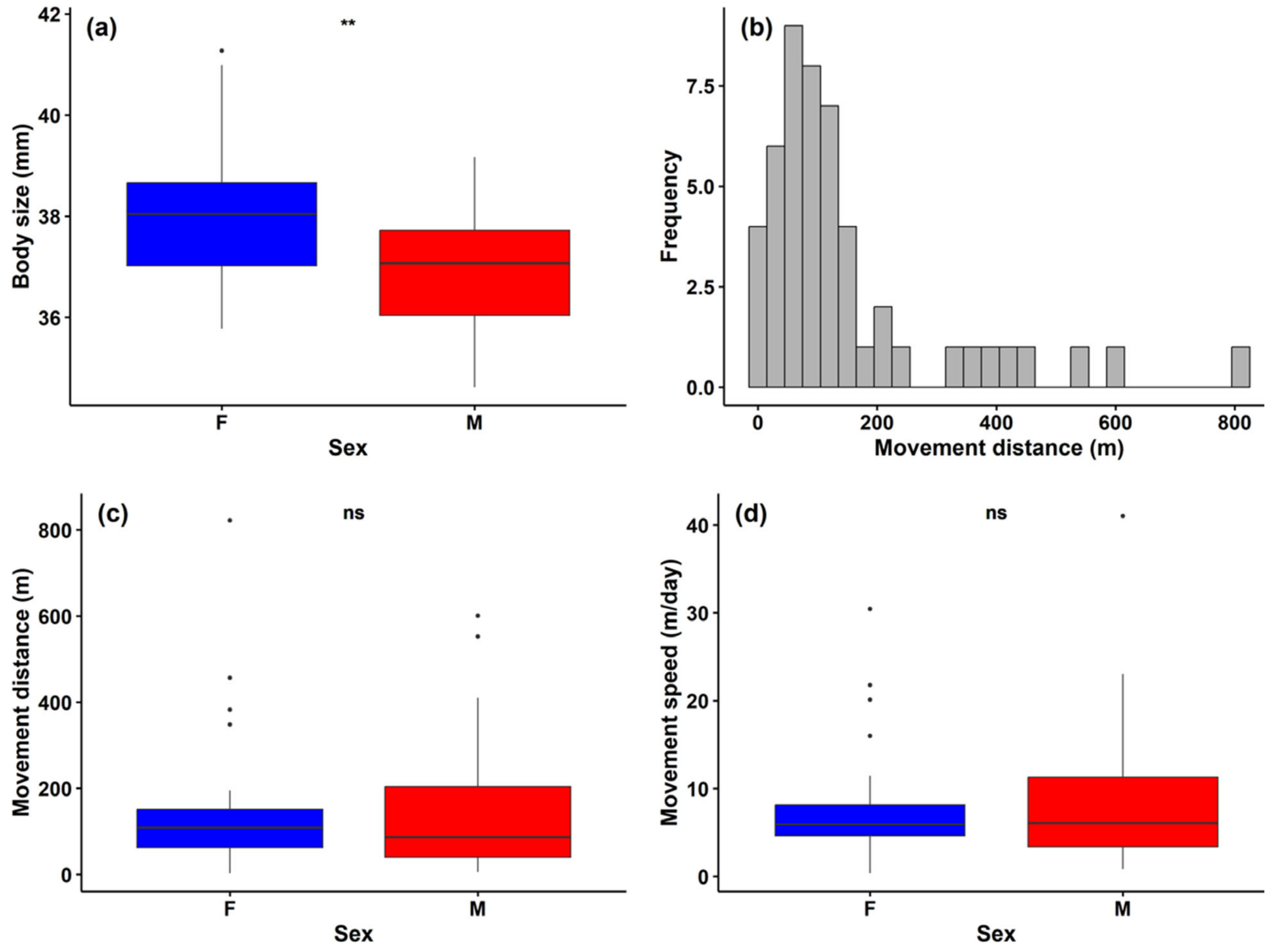

FIGURE 2 (a) Boxplot illustrating body length differences between sexes. As with panels (b) and (c), the horizontal line within each box indicates the median distance, with the box edges representing the interquartile range (IQR). Whiskers extend to 1.5 times the IQR, and outliers are plotted as individual points. Significant differences between sexes are indicated by two asterisks above the boxplots (ns $p > 0.05$; $^{**}p < 0.001$). (b) Histogram showing the distribution of total movement distances for all tracked beetles ($n = 50$). The x-axis represents the movement distance in metres, while the y-axis indicates the number of individuals. (c) Boxplot comparing total movement distances between sexes ($n = 29$ for males, $n = 21$ for females). (d) Boxplot comparing movement speeds (m/day) between sexes.

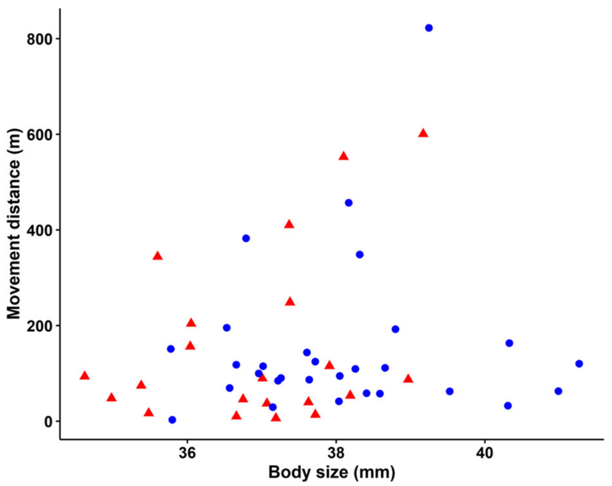

FIGURE 3 Scatterplot illustrating the relationship between body size (mm) and total movement distance (m). Red triangles represent female beetles, while males are depicted as blue circles.

$p = 0.67$) or sex ($F_{1,47} = 0.009$, $p = 0.92$) on the log-transformed cumulative distance moved.

DISCUSSION

Our results demonstrate a higher-than-expected dispersal ability for *C. cerdo* at the study site. This finding contrasts with earlier studies, such as the large-scale mark-recapture study conducted by Torres-Vila (2017) in Spain, which suggested a 'low-dispersal tendency and sedentary behaviour' for this species. The discrepancy may be attributed to several factors, including methodological differences and environmental context. As noted by Kissling et al. (2014), mark-recapture methods often underestimate movements compared to radio telemetry. In the study by Torres-Vila (2017), beetles were captured using baited traps and released on a single tree, where trap density—and thus recapture probability—decreased with distance from the release site. This setup likely contributed to the finding of limited mobility.

While we observed an average movement distance of 153 m, one individual travelled over 800 m. These results align with other studies suggesting considerable movement potential in *C. cerdo*, where 15% of individuals were tracked covering distances >2200 m (Drag & Cizek, 2018). However, the total distances recorded in our study were somewhat lower than those reported for Central European populations (Drag & Cizek, 2018). Differences in summer temperatures between Sweden and the Czech Republic may explain this discrepancy. Warmer temperatures are known to enhance insect activity and dispersal (Franzén & Nilsson, 2012), as shown in studies on *Osmoderma eremita*, where higher summer temperatures in Italy significantly increased dispersal rates compared to cooler regions like Sweden (Chiari et al., 2013). Large saproxylic beetles, such as *Lucanus cervus* has been shown to move >1700 m (Rink & Sinsch, 2007), *Scapanes australis* >1000 m (Beaudoin-Ollivier et al., 2003), *Osmoderma eremita* (Chiari et al., 2013) >1500 m and *Rosalia alpina* >1600 m (Drag et al., 2011). The comparison highlights that *C. cerdo*, far from being a poor disperser, exhibits similar mobility to other large beetles, challenging the notion of its sedentary nature.

The lack of statistically significant associations between body size and total distance moved is intriguing and contrasts with some studies on other insect species where body size has been positively associated with dispersal ability (Stevens et al., 2010). This finding underscores the complexity of factors influencing dispersal in *C. cerdo*. It suggests that environmental or behavioural factors may play a more significant role than morphology in determining movement patterns. The significant body size and weight differences between sexes, with larger and heavier females, likely reflect reproductive strategies. Larger body size in females is often associated with higher fecundity in insects, which may explain the tendency of females to remain in more stable habitats with sufficient resources (Ranius & Hedin, 2001). The non-significant difference in pronotum width between sexes suggests that locomotion and energy investment in flight are not the primary distinguishing factors between male and female *C. cerdo*, but rather that antenna length plays a more pivotal role for males to track females and their pheromones (Jaffar-Bandjee et al., 2020).

A significant challenge encountered in this study was that the transmitters were difficult to glue to the beetles and also rather heavy and large. This likely obscured the full range of beetle movement and may have resulted in an underestimation of dispersal distances. Despite being miniaturised to 0.13 g, the transmitters used in this study still represented approximately 10% of the beetles' body weight. This ratio exceeds the conventional '5% rule' often applied to vertebrates and can potentially affect the beetles' natural behaviours (Kissling et al., 2014; Wikelski et al., 2007). Recent work has highlighted that the impacts of tracking devices on terrestrial arthropods are often underestimated, with effects on both behaviour and survival that may bias movement data (Batsleer et al., 2020). Moreover, the transmitters attached with adhesive glue to the pronotum likely impeded the beetles' natural movement patterns. We also recorded several occasions of transmitter detachment, likely due to the beetles' interaction with their environment, further emphasising the limitations of current attachment methods. This is consistent with findings from previous studies, which highlight the need for improvements in transmitter design and attachment techniques to minimise interference with natural behaviour (Růžičková & Elek, 2023). Future studies might benefit from alternative tag attachment methods, such as UV-cured dental adhesives, which have shown promise in other insect tracking studies (Lioy et al., 2021). This technique has proven particularly effective with beetles and wasps; however, careful consideration of UV exposure intensity is necessary. Seven transmitters were lost and never recovered during our study. This suggests these beetles may have moved beyond the search area or experienced transmitter malfunctions, such as battery or antenna failures. Similar instances of tag loss due to transmitter malfunction have been documented in the radio telemetry study of the beetle *Carabus coriaceus* (Riecken & Raths, 1996).

Our observation that females outweighed males (1.53 vs. 1.27 g) contrasts with patterns reported from wild populations, where males are typically slightly heavier than females (Drag & Cizek, 2018). Several factors likely contribute to this difference. First, our sample was not random—we preferentially selected larger individuals capable of carrying radio transmitters, potentially biasing our morphological comparisons. Second, captive rearing conditions may affect sexual size dimorphism differently than natural conditions, potentially through differences in resource allocation or developmental cues (Houslay et al., 2015). These methodological and biological factors should be considered when comparing morphological patterns between captive and wild populations.

Our findings demonstrate that *C. cerdo* occasionally crossed the matrix between habitat fragments. Still, such movements were infrequent and primarily limited to short distances (Figure 1b). This highlights the species' limited dispersal capacity in fragmented landscapes, emphasising the critical role of ecological corridors in maintaining connectivity and facilitating gene flow (Fahrig, 2017). For reintroduction success, ensuring the availability of connected habitat patches is essential to support dispersal and population persistence (Moilanen & Hanski, 2001; Platek et al., 2019). Although the present study was limited in duration, the findings suggest the need for extended research across diverse landscapes to understand this species' movement ecology better. The successful emergence of adult *C. cerdo* from pupae has been observed in reintroduced populations at Tromtö and Björnö (J. Hedin, personal observation), indicating that the reintroduction has been successful. Incorporating these insights within a climate-smart conservation planning framework is essential for ensuring the long-term resilience of *C. cerdo* populations amidst ongoing environmental change (Forsman et al., 2024).

In conclusion, conservation efforts should prioritise monitoring the reintroduction sites to ensure the long-term success of reintroduced populations. Additionally, efforts should focus on preserving and creating large, suitable habitat patches within the dispersal range of *C. cerdo* to facilitate population connectivity and gene flow (Hanski, 2011). Rather than focusing solely on small-scale habitat connectivity, management strategies need to consider larger areas and ensure that critical oak habitats are sufficiently connected to support sustainable populations for this critically endangered species.

AUTHOR CONTRIBUTIONS

Markus Franzén: Conceptualization; supervision; formal analysis; funding acquisition; writing – original draft. **Nellie Jarl:** Methodology; writing – review and editing; data curation; project administration; formal analysis; validation; visualization; investigation. **Anders Forsman:** Conceptualization; funding acquisition; writing – review and editing; methodology; resources; supervision. **Jonas Hedin:** Conceptualization; funding acquisition; writing – review and editing; project administration; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study, along with associated R code and metadata descriptions, have been deposited in the Dryad Digital Repository. The dataset is accessible at Radio telemetry reveals extensive dispersal capabilities of reintroduced Great Capricorn beetles (Cerambyx cerdo) in oak habitats at their northern range limit. Reviewer URL: http://datadryad.org/stash/share/vMClztX3D9ItpwlLx7Puq5QkDWvJ4iWGulUujG5poBk (https://doi.org/10.5061/dryad.p2ngf1w21).

ETHICS STATEMENT

This study followed all relevant ethical guidelines for treating insects in scientific research. No ethical approval was required for the study involving *C. cerdo*. Permissions for fieldwork and the reintroduction programme were obtained from the provincial government of Blekinge.

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