

Using the movement patterns of reintroduced animals to improve reintroduction success

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Abstract Despite their importance to conservation, reintroductions are still a risky endeavor and tend to fail, highlighting the need for more efficient post-release monitoring techniques. Reintroduced animals are released into unfamiliar novel environments and must explore their surroundings to gain knowledge in order to survive. According to theory, knowledge gain should be followed by subsequent changes to the animal's movement behavior, making movement behavior an excellent indicator of reintroduction progress. We aim to conceptually describe a logical process that will enable the inclusion of behavior (in particular, movement behavior) in management decision-making post-reintroductions, and to do so, we provide four basic components that a manager should look for in the behaviors of released animals. The suggested components are release-site fidelity, recurring locations, proximity to other individuals, and individual variation in movement behavior. These components are by no means the only possible ones available to a manager, but they provide an efficient tool to understanding animals' decision-making based on ecological theory; namely, the exploration-exploitation trade-off that released animals go through, and which underlies their behavior. We demonstrate our conceptual approach using data from two ungulate species reintroduced in Israel: the Persian fallow deer *Dama mesopotamica* and the Arabian oryx *Oryx leucoryx* [Current Zoology 60 (4): 515–526, 2014].

Keywords Adaptive management, Arabian oryx, Conservation behavior, Exploration-exploitation trade-off, Persian fallow deer, Reintroductions

1 Introduction

Reintroductions of animals following their extirpation or extinction from the wild are a central aspect of ecosystem restoration (Polak and Saltz, 2011; Seddon et al., 2012), but despite their importance to conservation, reintroductions are still a complex and risky endeavor, often ending in failure (Short et al., 1992; Fischer and Lindenmayer, 2000). Increasing the success rate of reintroduction programs calls for better and more efficient post-release monitoring of the reintroduced animals (Fischer and Lindenmayer, 2000; Nichols and Williams, 2006; Armstrong and Seddon, 2008).

Reintroduced animals go through a unique process in which they are transported from their natal habitat and placed in a completely unfamiliar landscape (Bell, 2014). In such novel environments, gaining information is critical for survival (Frair et al., 2007). Therefore, following their release, reintroduced animals should perform exploratory movements aimed at constructing a spatial representation of the new environment in order

to allow for efficient resource utilization, predator avoidance, mate location and so forth (Burns, 2005; Russel et al., 2010; Berger-Tal and Avgar, 2012). However, exploration comes with a cost (e.g., energetic demands, higher predation risk, missed opportunities) and thus animals face a trade-off between their need to learn their environment and their need to exploit the already familiar resources (Eliassen et al., 2007; Berger-Tal et al., 2014). The exploration-exploitation dilemma is one of the most basic trade-offs in nature, and optimal performance usually requires different levels of exploration and exploitation depending on the level of knowledge the organism has of its environment (Berger-Tal et al., 2014). In other words, as an animal is becoming more familiar with its new environment, it should change its behavior accordingly. We term this process post release behavioral modification (PRBM). PRBM should include foraging, predator avoidance and social interactions, all of which are manifested in movement. According to theory, changes to an organism's internal state (e.g., the amount of knowledge it has) should trig-

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ger subsequent changes to the organism's movement behavior (Fryxell et al., 2008; Nathan et al., 2008). Consequently, the movement patterns of reintroduced animals and their temporal dynamics should be indicative of the establishment process of individual animals and the overall success of the release program.

Exploratory and knowledge-based movements represent two movement strategies at the extreme ends of one knowledge continuum, and in reintroduced animals we expect the movement component of the PRBM to change along this continuum with the accumulation of knowledge, shifting from mostly exploratory movements in an unfamiliar area to mostly knowledge-based movements within an established and familiar home range. Such patterns have been reported in the wild for a wide range of species (e.g., Crook, 2004; Selonen and Hanski, 2006; Fryxell et al., 2008; Gottert et al., 2010) and several simple cognitive mechanisms have been suggested to explain this behavioral shift (Van Moorter et al., 2009; Berger-Tal and Avgar, 2012). Therefore, the movement behavior of reintroduced animals can inform managers as to their approximate position on the knowledge continuum (i.e., whether the animals are still at the exploration stage where learning the environment is the highest priority, or whether the animals are familiar enough with the environment to be concentrating on the exploitation of resources). If the movements of released individuals do not reflect a gradual accumulation of knowledge, this may serve as a warning signal, alerting managers to the fact that the reintroduced population might not be acclimatizing to the new environment.

Post-release monitoring of reintroduced individuals is a fundamental part of the reintroduction process (IUCN 2012). It enables researchers to assess the reintroduction procedure and progress (Berger-Tal et al., 2012; Saltz et al., 2011), test a-priori hypotheses and questions regarding the reintroduced population and the ecosystem it is released into (Bar-David et al., 2005; Armstrong and Seddon, 2008), and provide the necessary data for an adaptive management approach and modeling (McCarthy et al., 2012). The rapid development of movement recording technologies, which enables managers to collect movement data on various spatial and temporal scales with increasing ease (Johnson et al., 2002; Cagnacci et al., 2010), has made the employment of tracking devices on released individuals a common practice (e.g., Matthews et al., 2013). Movement behavior is therefore not only an important indicator of reintroduction success, but is also increasingly available to managers of release programs, mak-

ing movement an extremely valuable tool for evaluating and managing reintroduction projects.

In this paper we suggest a simple and easy-to-implement behavioral approach to post-release monitoring of reintroduced animals. Specifically, we suggest incorporating simple analyses of released animals' movement behavior into the evaluation and decision-making processes of reintroduction programs. To do so we provide the basic components that a manager should look for in the movement behaviors of released animals. While these components are by no means the only possible ones available to managers, they provide an efficient tool to understanding animals' decision-making based on the exploration-exploitation trade-off that released animals go through, and which underlies their behavior. We then present an illustrative example of our conceptual approach using data from two ungulate species reintroduced in Israel: the Persian fallow deer *Dama mesopotamica* and the Arabian oryx *Oryx leucoryx*.

2 Movement Behavior Indicators for Reintroduction Success

In this section we list four major behavioral components that can be used as indicators for reintroduction success. All of these components can be at least partially discerned without the need for sophisticated statistical tools or knowledge, which makes them accessible to managers in the field. By continually monitoring one or more of these behavioral components, managers can get information on reintroduction progress in real time, allowing them to effectively use adaptive management techniques to improve reintroductions' success.

2.1 Release-site fidelity

Once released into the wild, animals can choose to stay in the vicinity of the release-site, or to disperse away from it. The decision of whether to disperse or not depends on the quality of the new habitat, on the animal's innate preferences, and on individual experience (Stamps and Swaisgood, 2007). Animals dispersing away from the release habitat can travel for extremely long distances, reducing their fitness during the critical post-release phase (Miller and Ballard, 1982; Reading and Clark, 1996). Furthermore, distant habitats may turn out to be less suitable for their survival (Stamps and Swaisgood, 2007). This has led managers to try various behavioral methods such as the use of conspecific decoys and other familiar cues to encourage released individuals to remain in the vicinity of the release-site (Bell, 2014). In some cases dispersal from the release site is

encouraged, especially when the release-site is well connected to other areas in which the species used to exist and when the species in question serves as an umbrella species (Bar-David et al., 2008). Regardless of if we want animals to disperse or to stay in the vicinity of the release site, the question of whether the released individuals exhibit post-release site fidelity is an important question with strong management implications.

During their exploratory phase, animals may favor dispersal behavior. Long-distance dispersal occurring shortly after the release may also be indicative of 'homing-behavior' (i.e. an attempt by the animal to return to its former home-range, be it captive or not), or despotic intra-specific interaction (Miller and Balard 1982; Saltz et al., 2000). Homing dispersal by reintroduced animals may result from hard releases or too short a residence in the habituation enclosure.

Once an animal has moved into the exploitation stage and established a home range, the chances of it performing a long-range dispersal are expected to be greatly reduced. Outside the context of reintroductions, site fidelity had been traditionally associated with territorial behavior and with the emergence of stable home ranges (Borger et al., 2008; Giuggioli et al., 2011) and several mathematical methods have been developed to infer it from animals' movement data (Turchin, 1998; Giuggioli and Bartumeus, 2012). However, in many cases a visual inspection of the animals' movement trajectories may be sufficient to assess whether reintroduced animals remain in the vicinity of the release-site or if and when they disperse away from it (see examples below).

2.2 Points of attraction: Recurring habitats and locations

Animals tend to spend more time, and return to, areas which they perceive as valuable (MacArthur and Pianka, 1966; Bar-David et al., 2009). Barring cases of ecological traps (where discrepancy between the cues that individuals use to assess habitat quality and the true quality of the habitat cause individuals to preferentially settle in habitats of lower quality; Schlaepfer et al., 2002), such areas usually provide them with high-quality resources such as food, water or shelter. These resource patches are extremely valuable to the management of reintroduced species, and can be used by managers to re-evaluate the spatial configuration of areas of conservation priorities, putting greater emphasis on the protection of areas that are deemed as valuable to the reintroduced species (or alternatively, in the case of ecological traps, these patches must be managed to negate their attraction to the

introduced individuals; Gilroy and Sutherland, 2007). In order to return to a high quality location, an animal clearly needs to find that location and consequently to evaluate it. Therefore, the number of recurring locations is generally expected to increase with the animal's accumulation of knowledge.

There are several statistical methods dedicated to identifying favorable areas (e.g., Fauchald and Tveraa, 2003; Barraquand and Benhamou, 2008; Benhamou and Riotte-Lambert, 2012; McClintock et al., 2012), but at a lower resolution, simply observing the movement path of an animal over time and the appearance of clusters of relocations may also reveal essential information on the locale and the nature of preferable areas to the reintroduced individuals. The spatial scale of reference is of great importance when looking for recurring habitats. A path that might look like having no recurring patterns at a small geographical scale might reveal such patterns once we look at the movement path at a larger scale (Morales and Ellner, 2002). Understanding the life history and ecology of the species in question and the landscape characteristics might give us a good indication as to what scales we should be looking for.

The spatio-temporal patterns of visits to recurring habitats can also give us important information about the nature of these habitats. For example, a relatively small area to which the animal is returning at a regular basis but stays only for short amounts time could represent a water source (and again, understanding the animal's ecology will serve to strengthen or weaken this hypothesis). In a similar way, a relatively small area to which the animal is returning to and stays for long periods of time may represent a shelter, and a larger area to which the animal is returning and stays for long periods of time may represent a foraging patch. Determining the actual attractor can, in many cases, be achieved by simply studying a map.

2.3 Proximity to other individuals

In many reintroductions, managers can obtain information regarding the locations of more than one individual. Such information is available if several animals with GPS tracking devices are released. In this case, the managers will have accurate and simultaneous high-resolution movement data for all tracked individuals. In some cases, additional information can be obtained from visual reports or from camera traps. Either way, managers may answer two important questions – do different individuals frequent the same areas, and if so, do they frequent them at the same time? In other words, do the released individuals socially engage with other

released individuals or with individuals already living in the wild? Proximity to other individuals can be a key factor influencing dispersal behavior of reintroduced animals (Le Gouar et al., 2012). In elk, *Cervus canadensis*, for example, individuals that aggregated into herds tended to disperse shorter distances than individuals who remained by themselves (Fryxell et al., 2008). A similar behavior was recorded in reintroduced black rhinoceros *Diceros bicornis*, where the scent of conspecifics in the release site reduced dispersal and encouraged the formation of home ranges (Linklater et al., 2006).

Some reintroduced animals are social by nature and often, in such cases, we want to encourage the formation of groups (such as herds) or maintain the group that was formed before the release. Destabilized social structures often result in reduced average fitness in the population (Flack et al., 2006; Wey et al., 2008). In highly social species, the continued existence or formation of stable groups means that the released animals are behaving like wild-born individuals, and is, therefore, indicative of a successful reintroduction. Other animals are solitary by nature, and evidence of individuals aggregating in certain locations may indicate that the release regime or landscape attributes altered the behavior of the reintroduced individuals, which may have negative consequences for the persistence of the entire population (Berger-Tal et al., 2011; Caro and Sherman, 2012). For example, the pre-release rearing experience of reintroduced Okarito kiwi *Apteryx rowi* in New Zealand increased their conspecific tolerance and resulted in larger group sizes post-release (Abbott et al., 2013¹); and the provision of supplementary food in spatially and temporally predictable feeding stations for reintroduced California condor, *Gymnogyps californianus*, resulted in the condors aggregating at feeding sites in concentrations that were never observed in the wild before (Walters et al., 2010).

Managers should also keep track of interactions between released individuals and resident individuals (either native to the area or from previous releases). In some cases, the existence of experienced conspecifics in the release area can facilitate learning in the newly released individuals, and hasten the formation of a stable home range (Dolev et al., 2002), while in other cases, especially in species exhibiting territorial behavior, res-

ident individuals may directly or indirectly drive new individuals away from the release area and prolong the exploration phase (Saltz et al., 2000). When looking at interactions of released individuals with conspecific, it is also important to consider the species reproductive behavior, and the timing of their breeding season.

2.4 Individual variation in movement behavior

Animals' 'temperament' or 'personality' refers to relatively consistent individual dispositions over time and across contexts that underlie and modulate the expression of behavior (McDougall et al., 2006). Temperament greatly influences reproductive behavior and survival by controlling key behaviors, including an animal's tendency to disperse and its reaction to novel situations (e.g., Sih et al., 2004; Smith and Blumstein, 2008; Cote et al., 2010). This has brought on the realization that understanding individual temperament may be critical for the success of reintroduction programs (McDougall et al., 2006).

Specifically, understanding the role of temperament in key behaviors of reintroduced individuals (e.g., movement, foraging or social behaviors) may allow managers to optimize the personality composition of each release cohort, in order to increase reintroduction success (Watters and Meehan, 2007). At later stages, when the released population begins to stabilize, this will also allow managers to increase the diversity of behaviors exhibited by the released population to increase their chances of coping with environmental changes (Caro and Sherman, 2012). However, temperament data is not always available prior to the release and may be species-specific. Therefore, any data collected on consistent individual variation in behavior of reintroduced individuals can greatly assist future releases of the same species.

In many cases, temperament traits can be divided into five major categories: shyness-boldness, exploration-avoidance, activity, sociability and aggressiveness (Reale et al., 2007). Perhaps the most important trait for reintroductions is the animal's tendency to explore. Some individuals may consistently venture into new areas and new habitats, while others will avoid new areas as much as possible and stay for much longer periods within familiar territories (Pinter-Wollman, 2009). Animals consistently approaching roads, settlements or

¹ Abbott R, Bell B, Nelson N, 2013. Improving conservation management of New Zealand's rarest kiwi *Apteryx rowi*: Effects of early rearing experience and optimal release group size. Abstracts of Behaviour 2013: Joint Meeting of the 33rd International Ethological Conference (IEC) and the Association for the Study of Animal Behaviour (ASAB), 4–8 August, 2013, Newcastle, UK.

other disturbing anthropogenic structures may be considered bolder than animals avoiding these disturbances (although they may also be affected by past habituation, which may be assessed based on the source of the animals: captivity, areas with intensive anthropogenic activity, or pristine). The activity of an individual may be estimated by calculating the total distance traversed by it in a given amount of time. Finally, it is also possible to approximate how social an individual is by looking at the animal's associations with other individuals, but in this case it is important to remember that interactions with individuals without tracking devices may occur, and thus any conclusion regarding an individual's sociality should be treated with caution unless all individuals are tagged.

3 An Illustrative Example

In this section we illustrate our proposed behavioral approach to post-release monitoring using data from two reintroduced species to show how it can be used to inform management policies. This example is of course limited in scope, depicting the movements of only a handful of individuals from two species, but it serves as a demonstration of how simple our proposed process is, and how easily achievable.

Our example addresses the movement ecology of two medium-sized ungulates that occupy different habitats and have different (resulting) social structures. The PRBM as expressed by the movement patterns of both species is expected to differ between the two species depending on the relative importance of two key factors: food and safety, which are components of the exploration-exploitation paradigm and also trade-off against each other. Persian fallow deer inhabit Mediterranean chaparral dominated by oak with well-developed undergrowth. They roam in small, loose association groups, varying in size from 1–5 individuals (Bar David et al., 2005). They are subject to predation (Zidon et al., 2009; Saltz et al., 2011), and safety is achieved by concealment and cautious movement. Oryx, on the other hand, inhabit hyper-arid open deserts where food is concentrated in patches along dry-riverbeds that are far apart. Oryx are highly social and live in closed membership groups of up to several dozen individuals, with a clear hierarchy. The habitat they occupy is mostly open desert plains with low bushes in isolated patches. Thus, refuge is literally not available. Furthermore, Arabian oryx have a strongly reflective white coat making them highly visible to predators. However, predators inhabiting their range (wolves and foxes) pose little threat to

adults, and the young are actively protected by group members (Stewart, 1963). Thus, in terms of the food-safety tradeoff, safety is a more important concern for fallow deer, while for the oryx food (in the form of patches that are productive enough to support the group) is more vital.

We present data on the fine-scale movements of three Persian fallow deer females and three Arabian oryx females. The fallow deer were released between October 2009 and October 2011 into the Nahal Kziv Nature Reserve, a Mediterranean woodland habitat in the north of Israel. The oryx were released between November 2010 and August 2011 to Ein Shachak in the Arava rift valley, a hyper-arid environment composed of mostly open area with patches of sparse acacia trees and low bushes. Both deer and oryx originated from captive-bred herds and were placed in an on-site habituation enclosure for ca. three months prior to release. The animals were equipped with GPS collars ('Africa Wildlife Tracking', Pretoria, South-Africa) that were programmed to record a location every 10–15 minutes for 1–3 months following the release and from then on the collars recorded one position per day, except for the last 5 days of each month, during which the collars recorded a location every 15 minutes.

3.1 General patterns

All three fallow deer stayed in close vicinity to the release enclosure, never moving more than 1 km away from it for several months following their release, after which two of the deer shifted the center of their activity and moved away from the area surrounding the enclosure (Fig. 1). The shift to a new location was an abrupt single event lasting less than two days (data not shown). One deer remained close to the release enclosure. All three deer substantially increased the size of the area they regularly traverse with time (Fig. 1). In an unfamiliar environment, the spatial scale the animal is reacting to is limited to the area it perceives. In contrast, when the landscape is familiar, an animal can move within its home range deliberately using its spatial memory thereby responding to the environment on a much larger scale (Fagan et al., 2013). Indeed, further analyses of the fallow deer's activity budget show a shift from mostly slow foraging movement in an unfamiliar environment to a more bi-modal behavior in a familiar landscape of either walking directly, most probably between resource patches, or concentrated movements within one location, most probably within resource patches (Berger-Tal, 2013; Fig. 2).

The oryx exhibited very different movement patterns.

After their release, the oryx walked in long and very straight lines, covering large distances. Interspersed with the long bouts were periods of very limited movement, suggesting these were resting stops (Fig. 3). Within a few weeks of their release, all oryx already

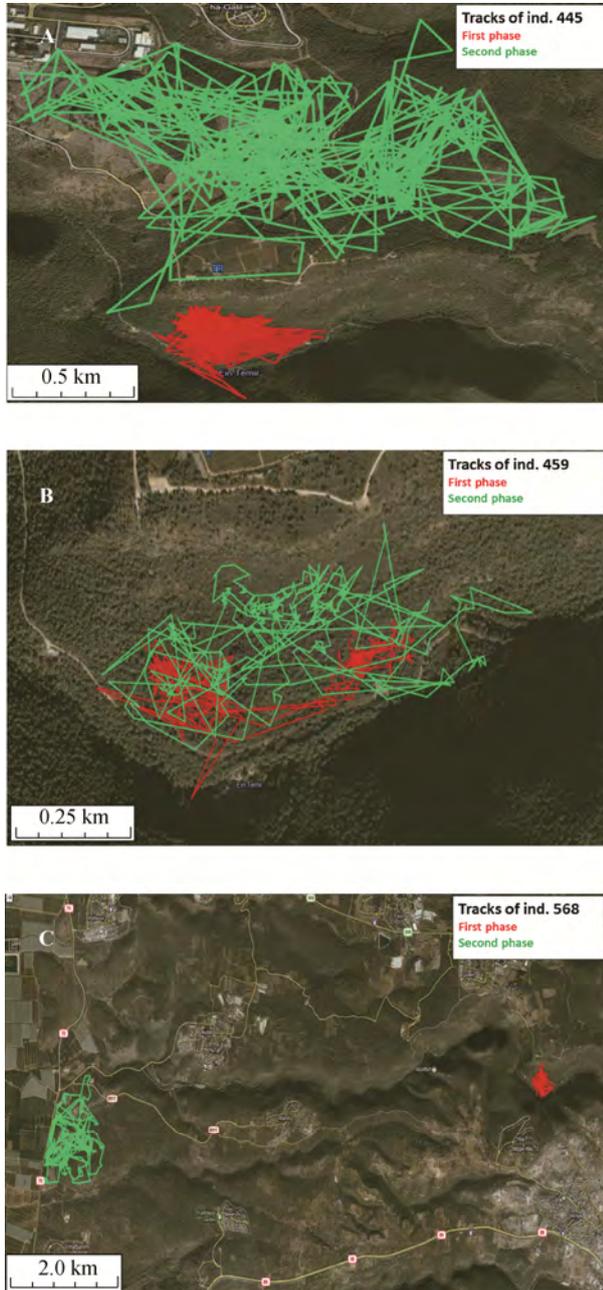


Fig. 1 The movement paths of three Persian fallow deer females: (A) #445, (B) #459 and (C) #568

The red path is the movement path immediately after the deer release into the wild for a duration of 3 months (#445), or approximately a week (1,000 locations, #459 and #568). The green path is the last movement path recorded by the GPS collars, for a duration of 3 months (#445), or approximately a week (1,000 locations, #459 and #568). The locations were taken at a rate of one location per 15 minutes. The maps were generated using Google maps and “GPS Visualizer”, a free map generator available online (<http://www.gpsvisualizer.com/>).

spent most of their time within a limited area (i.e., they created stable home ranges; data not shown). However, even though the oryx spent most of their time in confined areas, they continued, once every few weeks, to

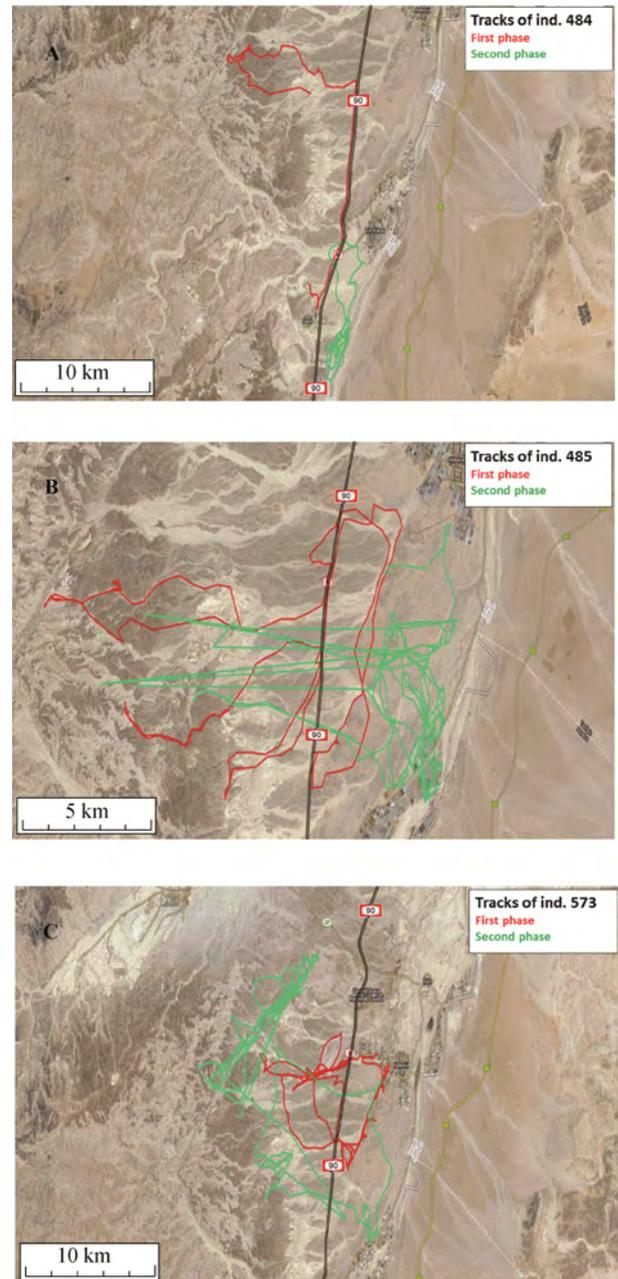


Fig. 2 The movement paths of three Arabian oryx females: (A) #484, (B) #485, and (C) #573

The red path is the movement path immediately after the oryx release into the wild for a duration of approximately a week (1,000 locations). The green path is the last movement path recorded by the GPS collars, also for a duration of approximately a week (1,000 locations). The black line represents road 90 - a major road that runs through the study area. The locations were taken at a rate of one location per 10 minutes for the green path, and one location per 15 minutes for the red path. The maps were generated using Google maps and “GPS Visualizer”, a free map generator available online (<http://www.gpsvisualizer.com/>).

carry out ‘exploratory bouts’ in which they walked very long distances (reaching up to 50 km and more) into

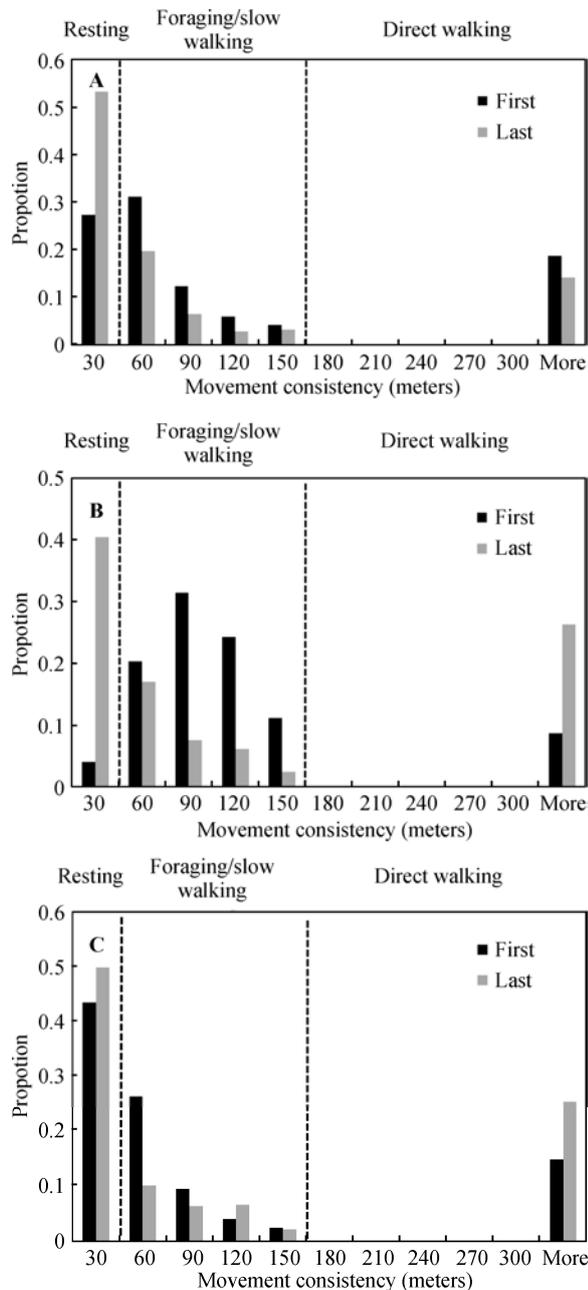


Fig. 3 The frequency of different movement activity modes (Resting, foraging and slow-walking, direct walking) of three Persian fallow deer females: (A) #445, (B) #459, and (C) #568, derived using the First-passage Radial Scaling of Time (FiRST) method (Zidon 2012)

The method uses the consistency of movement (where consistency is defined as the tendency to move directionally for a long time) to discover and characterize changes in Canonical Activity Modes (CAMs – characteristic movement patterns that within a particular context, such as the species and type of environment, define specific behaviors such as foraging, walking, resting, etc., Getz and Saltz, 2008). See Zidon (2012) for additional details on this method. Black bars represent the first 1000 location points after the deer release. Grey bars represent the last 1000 location points taken by the GPS collars.

unfamiliar landscapes, only to return to their home range a few days later.

In terms of their activity budget, the oryx showed a somewhat reversed trend to the deer – in a novel environment the oryx displayed a mostly bi-modal movement behavior: resting/slowly foraging and long-range directional walking (except for one female who showed almost no direct walking). In a familiar environment the frequency of direct walks was greatly reduced, while the frequency of resting and/or slow foraging was increased (Fig. 4). The oryx live in a much patchier environment than the fallow deer, where there is a sharp contrast between the inhospitable desert matrix, and the resource patches that usually consist of one or several acacia trees. Despite being random, exploratory movement through the harsh matrix should not be slow and tortuous but rather straight and fast. When oryx find a resource patch they can assess it by utilizing it, i.e., by foraging in it, which can explain the bi-modal behavior that emerges during the oryx exploratory phase. Once familiar with the landscape and aware of the locations of the resource patches, the oryx can reduce their movement between patches, taking the most direct and efficient routes, and spending more time within the patches, increasing their resting and foraging behaviors in the process. These results add support to the many studies showing that the physical properties of the environment have a strong influence on animal movement behavior (e.g., Turchin, 1991; Wiens et al., 1993).

3.2 Release site fidelity

All deer stayed for at least several months in the area surrounding the release enclosure. This pattern was evident in most females released in this project (data not shown). The dispersal away from the release area seems to be a single and relatively short event, but a larger sample size is needed to determine the factors that may trigger this event.

Although oryx spent the same amount of time as the fallow deer in a habituation enclosure, they showed no release-site fidelity whatsoever. All three released females (as well as other individuals whose movements are not reported here) left the area of the release site immediately upon release. This is to be expected from a species that evolved in hyper arid environments where productivity is highly variable over space and time and exploration becomes a key factor in the animal’s fitness.

3.3 Recurring locations

In Figure 5 we show the movement path of one fallow deer female (female #445) on: A. the week following the release; B. one week approximately one year

later. The path is divided to seven segments of different colors, each representing a different day within this week. To keep the description tractable and simple we only show this one female, however these patterns were very robust and exhibited by the other two females as well. In the week following the release, female #445 covered more or less the same area every day of the week and showed no preference for one location or

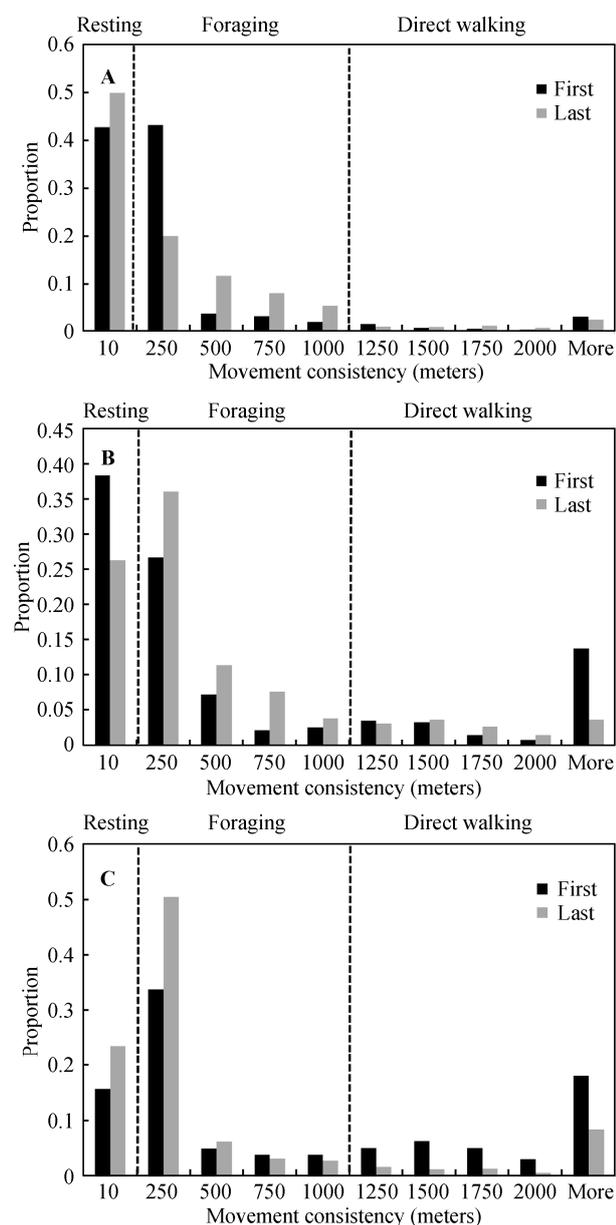


Fig. 4 The frequency of different movement activity modes (Resting, foraging and slow-walking, direct walking) of three Arabian oryx females: (A) #484, (B) #485, and (C) #573, derived using the First-passage Radial Scaling of Time (FiRST) method (Zidon, 2012; see Fig. 3)

Black bars represent the first 1,000 location points after the deer release. Grey bars represent the last 1,000 location points taken by the GPS collars.

another. A year later, this female covered a much larger area during the week, passing through different parts of her home range every day. However, there were several areas to which the female kept returning to in most, if not all, days. The black circle in the map indicates on the core of the female's home range. The female returned to this area every day, and within this core area it is possible to recognize specific spots in which the female spent most of her time. From their small size, and the fact that these spots are located within dense vegetation, it is probable to assume these areas served for bedding/shelter. The white circles are around two areas which female #445 visited on 4 different days of the recorded week. These are open areas and this suggests that these are favorable foraging spots in which the female grazed. Being in open areas renders the fallow deer more exposed to both predators and humans (who may be perceived as a risk). Indeed, the movement data shows that the female never visited these areas during

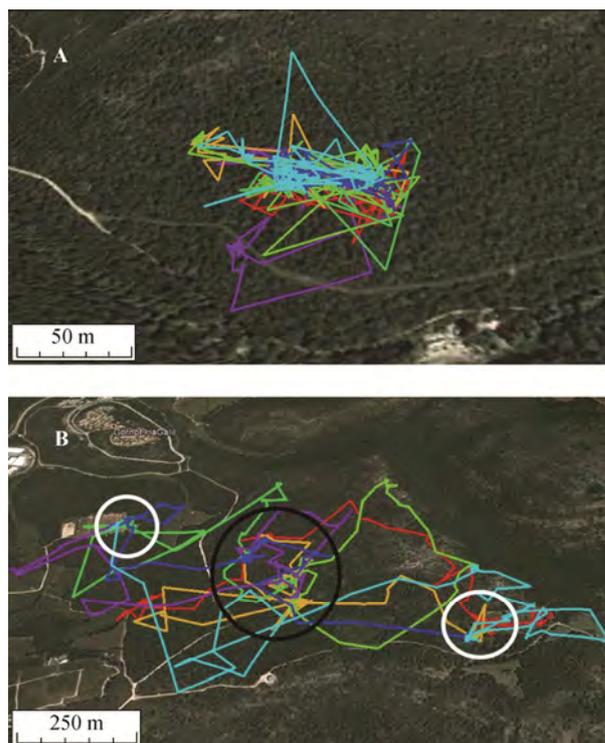


Fig. 5 The movement path of one fallow deer female (female #445) on: (A) the week following the release; (B) one week approximately one year later

The path is divided into seven segments of different colors, each representing a different day within this week. The black circle in the map indicates on the core of the female's home range to which the female returned every day. The white circles are around two areas which the female visited on 4 different days of the week. The map was created using Google earth and "GPS Visualizer", a free map generator available online (<http://www.gpsvisualizer.com/>).

daytime, and instead always used the cover of darkness during twilight hours and all through the night (data not shown).

Figure 6 shows the movement path of one oryx female (female #485) on: A. the week following the release; B. one week approximately 20 months later. As in the fallow deer example, these patterns represent well the movement patterns shown by the other two females. Immediately following her release, during her exploratory phase, Female #485 was persistent and directional in her movement and never returned to a location she visited before. Due to the oryx's preference of walking in dry river beds or along roads, paths from different days sometimes partly overlap, but the female never stopped in the same place more than once within this week. The female's movements 20 months later were more restricted to her home range east of road 90, although one daily excursion several kilometers west of the road can be seen during this week. The white circles

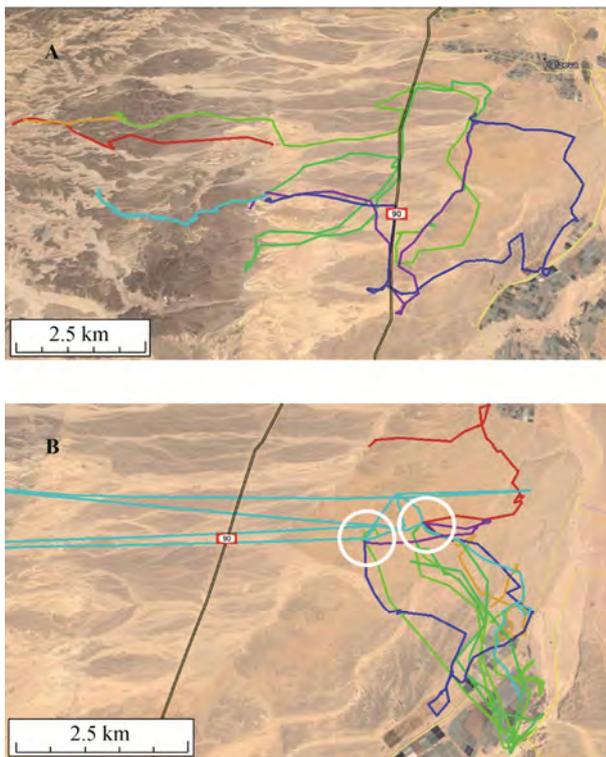


Fig. 6 The movement path of one oryx female (female #485) on: (A) the week following the release; (B) one week approximately 20 months later

The path is divided into seven segments of different colors, each representing a different day within this week. The black line represents road 90 - a major road that runs through the study area. The white circles represent two specific locations to which the oryx returned to several days during the week. The map was created using Google earth and "GPS Visualizer", a free map generator available online (<http://www.gpsvisualizer.com/>).

denote two specific locations to which the oryx returned to several days during this week. A closer inspection of these locations reveals that these are large acacia trees which probably served the oryx as regular foraging and shaded resting spots.

3.4 Proximity to other individuals and temperament

The movement paths of any of the fallow deer females (as well as of other females we have more limited data on) never coincided more than briefly and there seems to have been no long-lasting contact among the released females. Several collared and uncollared females have been documented by camera traps, and they were almost always alone or accompanied by a young fawn.

There are definitely large differences between deer individuals in their dispersal patterns away from the release-site area. One individual did not disperse at all, the other two dispersed to varying distances. However, since we only have complete data sets for three individuals, we cannot make any reliable estimates about the temperaments of the released individuals.

Despite their social nature, the released oryx females did not join the existing herd of a few dozen oryx that roams in the area. Still, in some cases it is clear that social behavior dictated the movement paths of the released individuals. A few weeks after her release, female #573 joined female #485 who was released 10 months earlier, and for at least several months their movement paths were identical (both time- and space-wise). Female # 485 was also spotted several times with an unknown male and gave birth during the 20 months her movement was tracked, thus these individuals formed a small herd of three adults and one juvenile.

As with the fallow deer, we could not make any reliable estimates about the temperaments of the released individuals due to our small sample size. However, it is clear that in general, oryx individuals are very explorative in their nature, constantly venturing into novel landscapes.

3.5 Management implications and recommendations

The deer's movement behavior confirms that the released females have "settled in" within a stable home range. We found a clear shift in the deer's behavior from mostly slow and constant movements restricted to a small area around the release enclosure, to a mostly bi-modal movement strategy that consisted of direct walks within a large home-range and very concentrated movements within restricted areas. The former strongly suggests that the females were initially mainly exploring the new landscape, while the latter indicates on

movement between and within established resource patches. This and the emergence of recurring locations to which the females kept returning at a regular basis reflects the existence of a PRBM process culminating in the establishment of a home-range with which they are familiar enabling them to exploit it in a seemingly efficient pattern. Thus, the PRBM has been completed and, at least for these females, the reintroduction process was successful.

The movement behavior of the released deer suggests that in future releases, managers can expect fallow deer females to remain in the vicinity of the release enclosure for several months after their release. This calls for specific long-term management intervention in this area. A major cause of fallow deer reintroduction failures in the past few years has been high predation levels in the first few weeks after the deer's release (Saltz et al., 2011). The fact that we now know that during these weeks the deer stay close to the habituation enclosure may allow for an efficient predator control program in the vicinity of the enclosure during the deer's sensitive period. This area is also popular with hikers. So far, releases were always scheduled outside peak tourist season. However, our data shows that it is best to schedule the releases a few months before peak season, in order to reduce possible stress caused by a large amount of hikers in the area while the fallow deer are still in their primary exploration phase around the enclosure. These two actions may greatly improve post-release survival of these endangered species.

In the oryx case, despite not joining the stable herd that roams the area and despite their frequent exploratory bouts, the clear behavioral shift in the released individuals' movement patterns strongly indicates that the oryx have "settled in" and are no longer in their exploration phase. The creation of a new "mini-herd" also supports the fact that the oryx have modified their behavior to fit the natural landscape they occupied.

The knowledge that oryx go on exploratory bouts, even after they have a home range, has strong implications regarding the need for the creation of safe passages along route 90 – a major road that runs along the entire rift valley. The oryx movement paths indicate that they do not cross the road randomly, but rather prefer to cross at specific locations (data not shown). Currently, the movement data from the oryx releases is being used to plan the optimal locations for the construction of safe passages across route 90 (Ben-Aharon, N., Pers. Comm.)

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