Water requirements as a bottleneck in the reintroduction of European roe deer to the southern edge of its range

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Abstract: Success rates of reintroduction programs are low, often owing to a lack of knowledge of site-specific ecological requirements. A reintroduction program of European roe deer (*Capreolus capreolus* (L., 1758)) in a dry Mediterranean region in Israel provides an opportunity to study the bottleneck effect of water requirements on a mesic-adapted species. Four does were hand-reared and released in a 10 ha site consisting of an early succession scrubland and a mature oak forest. We measured daily energy expenditure (DEE) and water turnover (WTO) using the doubly labeled water technique during summer and winter. DEE was similar in the summer and winter, but there was a significant difference in WTO and in the source of gained water. In winter, WTO was 3.3 L/day, of which 67% was obtained from vegetation. In summer, WTO dropped to 2.1 L/day, of which only 20% was obtained from the diet and 76% was gained from drinking. When the water source was moved to a nonpreferred habitat, drinking frequency dropped significantly, but water consumption remained constant. In a dry Mediterranean environment, availability of free water is both a physiological contraint and a behavioral constraint for roe deer. This study demonstrates the importance of physiological and behavioral feasibility studies for reintroduction programs.

Résumé : Le taux de succès des programmes de réintroduction sont bas, souvent à cause de l'ignorance des besoins écologiques spécifiques au site. Un programme de réintroduction du chevreuil d'Europe (*Capreolus capreolus* (L., 1758)) dans une région méditerranéenne sèche en Israël nous fournit l'occasion d'étudier le goulot d'étranglement que représentent les besoins en eau pour une espèce adaptée aux milieux mésiques. Quatre biches élevées à la main ont été relâchées sur un site de 10 ha comprenant un maquis encore à un stade jeune de la succession et une forêt de chênes à maturité. Nous avons mesuré durant l'été et l'hiver la dépense journalière d'énergie (DEE) et le taux de renouvellement de l'eau (WTO) à l'aide de la technique de l'eau doublement marquée. Les DEE sont semblables en été et en hiver, mais il existe une différence significative entre les valeurs de WTO et les sources de l'eau utilisées. En hiver, le WTO est de 3,3 L/jour dont 67 % provient de la végétation. En été, le WTO tombe à 2,1 L/jour dont seulement 20 % provient du régime alimentaire et 76 % est obtenu par ingurtitation. Lorsque la source d'eau est déplacée vers un habitat non préféré, la fréquence d'ingurgitation diminue significativement, mais la consommation d'eau se maintient constante. Dans un milieu méditerranéen sec, la disponibilité d'eau libre représente une contrainte à la fois physiologique et comportementale pour le chevreuil. Notre étude démontre l'importance des études physiologiques et comportementales de faisabilité dans les programmes de réintroduction.

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Introduction

Reintroduction programs have become one of the major conservation methods worldwide for protecting endangered species and rehabilitating habitats (Gipps 1991). Unfortunately, their success rate is generally low (Fischer and Lindenmayer 2000). A major problem can arise when little is known about the ecological requirements of the reintroduced species (e.g., Thouless et al. 1988). The likelihood of suc-

cessful reintroductions may improve if comprehensive feasibility studies are carried out (Wallace 2000). However, difficulties arising from limited resources, urgency of the recovery task, and concerns over the effects of invasive research on rare species have often limited this crucial phase (Clark et al. 1994). Even in cases where feasibility studies have been carried out, they rarely attempt to define ecological requirements at each of the releasing sites. It has been demonstrated that habitat quality is the most important factor

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which determines reintroduction success (Griffith et al. 1989; Wolf et al. 1996). Therefore, species requirements should be studied in the context of the habitats that it will be introduced to. This study addresses the reintroduction of the European roe deer (*Capreolus capreolus* (L., 1758)) in Israel.

Roe deer have been locally extinct in the eastern Mediterranean as a result of hunting and habitat loss since the beginning of the 19th century (in Jordan; Quemsiyeh et al. 1996), as well as since the 20th century in Lebanon, Israel, Syria, and Iraq (Aharoni 1943; Harrison and Bates 1991). Their current range extends throughout most of Europe (Andersen et al. 1998). Roe deer can have a significant impact on the structure and dynamics of vegetation communities (e.g., Ammer 1996; Carranza and Mateos-Quesada 2001; Partl et al. 2002), are an important prey species for a variety of large carnivore species (Aanes et al. 1998; Jarnemo and Liberg 2005), and are likely to aid in carnivore rehabilitation programs (e.g., Boitani 1992). It has therefore been proposed that roe deer are keystone species (Cederlund et al. 1998).

Many European countries have been successful in actively preserving and reintroducing this species to their historic range after being locally extirpated, e.g., in Britain (Prior 1995), France (Maillard et al. 2002), Italy (Boitani 1992; Dupanloup et al. 2002), Portugal (Jose et al. 2001; Vernesi et al. 2002), Scandinavia (Liberg et al. 1994), and Spain (Braza et al. 1989; Rosell et al. 1996). Successful reintroduction programs combined with the natural expansion of distributions have enabled the roe deer to reinhabit a wide range of biomes, from the Arctic to the Mediterranean (Andersen et al. 1998). This has led to the assumption that they would easily adapt if released into former areas that they occupied in the eastern Mediterranean (Saltz et al. 1995). Current regulations on hunting and protection of nature reserves have made it possible to consider a reintroduction program of this species in Israel. Consequently, during the 1980s and 1990s, the Israeli Nature and National Parks Protection Authority (INNPPA) imported a group of roe deer from several European countries (Holland, France, Italy, and Hungary) to establish a breeding colony in the Hai Bar Nature Reserve on Mount Carmel.

Reintroduction programs carried out at the extreme edge of a species natural distribution are known to have lower probabilities of success, mainly because of low habitat quality (Griffith et al. 1989; Wolf et al. 1996). In northern Europe, the limiting factors are the cold winters, short growing seasons, and high snow accumulation (Holand et al. 1998). However, in xeric sites such as the forests of Spain (the southern limit of the roe deer's western Palaearctic range), habitat constraints related to heat and dryness restrict roe deer numbers and distribution; they prefer the more mesic forested mountains (Sáez-Royuela and Tellería 1991; Tellería and Virgós 1997; Virgós and Tellería 1998). In the eastern Mediterranean, the scarcity of water sources may pose a severe constraint, especially because birth, lactation, and rut all occur during the summer (Andersen et al. 1998) when (*i*) most of the water sources and natural vegetation are dry and (*ii*) temperatures are high.

The dependence of ungulates on free water has been studied mostly in arid environments (e.g., mule deer, *Odocoileus hemionus* (Rafinesque, 1817): Hervert and Krausman 1986; Sánchez-Rojas and Gallina 2000*a*, 2000*b*; white-tailed deer, *Odocoileus virginianus* (Zimmermann, 1780): Bello et al. 2004; mountain gazelles, *Gazella gazella* (Pallas, 1766): Tatwany and Goldspink 1996; Arabian oryx, *Oryx leucoryx* (Pallas, 1777): Williams et al. 2001), but knowledge regarding the water demands of ungulates in nonarid, but water restricted, environments is limited (mountain gazelle: Baharav 1983; mule deer: Boroski and Mossman 1996, 1998; Bowyer et al. 2001). Despite the large number of research carried out on roe deer, the availability of free water as a direct, physiological constraint has been overlooked. In Israel, and across the Mediterranean zone, during the past 100 years, many of the free-water sources that used to be available to wildlife have been taken up by human demand. Therefore, determining the water needs of roe deer in dry Mediterranean habitats is fundamental and must be determined prior to conducting a full-scale release.

Materials and methods

Animals and study site

Four does, born in the Hai Bar Carmel reserve, were hand-reared (two in 2001 and two in 2002), and at the age of 6–8 months were released into a 10 ha study site. We chose females, rather than males, because hand-reared males can become dangerously aggressive when they reach maturity (Prior 1995). The hand-rearing procedure and experiment design were under license from the INNPPA and the Ethics Committee of the University of Haifa (Wallach et al. 2007).

The site was within the boundaries of the Hai-Bar Nature Reserve on the Carmel ridge (34°97′N, 32°72′E) and consisted of two habitats: (1) an early succession scrubland recovering from a fire (2 ha) in which sageleaf rockrose (*Cistus salvifolius* L.) and Mediterranean thorny broom (*Calycotome villosa* (Poir.) Link.)) were abundant (i.e., "young habitat") and (2) a mature oak forest (8 ha) dominated by Palestine oak (*Quercus calliprinos* Webb.) and evergreen pistache or mastic tree (*Pistacia lentiscus* L.) (i.e., "mature habitat"). We classified seasons as summer (June–November) for both the summer and autumn (high temperatures of 20–32 °C, no rainfall, and no annuals or new growth), and winter (December–May) for both the winter and spring (cool temperatures of 9–20 °C, rain is common, and annuals and new growth of perennials are available). However, we also separated these two seasons into four to account for annual temperature changes when we studied water consumptions. Throughout the research (2003–2004), the deer were accessed on a daily basis, enabling them to remain habituated to the observer (A.D.W.). It was therefore possible to locate, closely observe, and physically contact the deer in natural conditions without causing them stress. The deer fed on the vegetation available in the study site and did not receive additional food during the trials. Free water was available ad libitum. They were weighed at the beginning and end of each trial (modified sheep field scales with an accuracy of ±0.05 kg; AB100P, Shekel, Israel). All four does were mature (≥2 years old, 22–23 kg) during the experimental period. Apart from a single trial (see doubly labeled water), which was conducted with two does at a time, all four does were monitored together.

Water as a physiological constraint

We studied the water consumption of roe deer in two different ways: (1) estimating water turnover (WTO) from the deuterium elimination rate after the injection of doubly labeled water (DLW; Nagy and Costa 1980) and (2) estimating the water content of their diet through behavioral observations of foraging and the evaluation of dietary water content, as well as measuring daily free-water consumption.

Measurement of WTO and daily energy expenditure (DEE)

We estimated from noninvasive urine samples (Parker et al. 1999) the WTO, percent body water, and DEE using the DLW technique (Lifson and McClintock 1966; Speakman 1997; 1998). Two individuals were measured in 2003 and two in 2004, thus all deer were 2 years old at the time of the experiment. Measurements took place during both winter (February–March) and summer (September). One doe suffered from severe stress and minor injuries during the winter injection operation in 2003, and therefore was excluded from the analysis. The day prior to the injection, a urine sample was collected (by following the doe until she urinated into a plastic tray that was held underneath her) to determine isotope background levels (method D from Speakman and Racey 1987). The next day, the deer were maneuvered into a small enclosure (2 m × 3 m) and were restrained to the ground until injected with DLW (2.3 parts 90% enriched ^{18}O water (Enritech Ltd., Rehovot, Israel) and one part 99.9% enriched ^{2}H water (MSD Isotopes Inc., Pointe-Claire, Quebec, Canada)) (intravenous ~0.2 g/kg body mass). The whole process took 5 min, after which the does were released. Since roe deer are especially prone to stress, we neither kept them restrained nor did we recapture them to obtain an initial enriched sample (as the "plateau" technique would require). Instead, we used the "intercept" technique to extrapolate values of initial enrichment, obtained from a series of post-dose urine samples (Speakman 1997). During the 7 days after the injection, three urine samples were collected at approximately the same time each day to minimize sampling interval errors (Speakman and Racey 1988). The average precision of the analyzed samples was 48 min (range 0–3 h). Urine samples were immediately flame-sealed in glass capillary tubes. They were then vacuum distilled (Nagy 1983), and the water from the resulting distillates was used to produce CO_2 and H_2 (Speakman et al. 1990, Speakman and Król 2005). Isotope ratios of ^{18}O:^{16}O and ^{2}H:^{1}H were then analyzed using gas source isotope ratio mass spectrometers (Optima and Isochrom μG; Micromass Ltd., Manchester, UK), prior to calculation of DEE (Lemen and Speakman 1997). We used the two-pool model (eq. 7.43 from Speakman 1997) as recommended for mammals weighing >5–10 kg (Speakman 1993). WTO values were calculated according to Nagy and Costa (1980).

Estimating water obtained from diet

The diet of free-ranged, hand-reared deer is considered equivalent to mother-reared deer (Spalinger et al. 1997; Tixier et al. 1997, 1998; Parker et al. 1999). We studied the diet composition and feeding activity of does to estimate preformed water intake during the winter and summer in the two habitats. Daily feeding activity (defined as the amount of time the deer spent consuming food during a day) and

drinking activity (the time and frequency of drinking events) were determined over a 24 h period. Each observation was conducted in 12–14 h sessions, for day and night observations (apart from one 25 h session). Six full-day observations were conducted in the summer and three full-day observations were conducted in the winter. While the deer were active, the proportion of time spent feeding was measured by repeatedly observing 10 min of activity during different hours of the day (n = 47 observations). Their diet composition was expressed as the proportion of time spent consuming each plant species, which was determined by observing a minimum of 10 min of active feeding each day for a 2–3 week period, in each habitat and season for each doe (mean total observation length per season of a deer was 3.4 h in each habitat). These time intervals were chosen based on preliminary optimization tests (A.D. Wallach, unpublished data). To provide a quantitative estimate of intake rates, we presented the deer with food items during a fixed period and compared the mass of the food before and after consumption (Tixier et al. 1997). Dominant plants in their diet (>2% of the diet) were collected in each season and the water content of each food item was measured by drying samples of food to constant mass at 60 °C (drying oven; Memmert GmbH + Co. KG, Schwabach, Germany). The amount of water that the deer obtained from forage (W_{deer}) was then determined according to the following equation:

$$W_{\text{deer}} = \sum_{i=1}^{S} T(t_{p_i} v_i W_{p_i})$$

where i is the ith food item in the deer's diet, T is the daily feeding activity, t_{p_i} is the proportion of time spent feeding on the ith food item, v_i is the intake rates of the ith plant species, and W_{p_i} is the proportion of water in the ith plant species (volume/g).

Water can also be obtained from the diet by consuming plants that are wet from rain or dew (especially in the winter) and from metabolic water production. The additional amount of water obtained in the winter when leaves are wet was estimated by weighing the leaves of four different plant species before and after spraying them with water. The maximum amount of metabolic water that can be produced was estimated by multiplying the DLW estimate of DEE by 0.032 g H_2O/kJ (from the oxidation of starch; Willmer et al. 2000).

Free-water consumption

The pooled amount of water consumed by all four does was recorded daily for a period of 2–4 weeks, four times a year (winter: January–February; spring: April–May; summer: August–September; autumn: November), in both habitats. We provided water in buckets and measured the evaporation rates in a control bucket covered with a top wire mesh (2 cm × 2 cm holes) that prevented drinking. In winter, we measured water consumption only on dry days when there were no puddles. We then divided by 4 the group's water consumption to establish a mean individual water consumption rate. We recorded daily minimum and maximum temperatures throughout the trials. To determine the standard deviation within the group, we measured the daily water consumption of each doe individually for a pe-

riod of 72 h (in 2 sets of 36 h) in the summer (by removing three of the four deer from the study area into a separate enclosure). To determine the water drinking frequency, we pooled all drinking events that were observed in the 24 h period and calculated the proportion of drinking events that occurred at half-hour intervals from the total number of drinking events. We then averaged the proportions of each half-hour interval for all does.

The effect of free-water availability on deer behavior

The location of the water source in the wild might not coincide with the habitat preference of the deer and this might have a significant effect on the accessibility of this resource. We therefore studied the effect of the location of the water source on habitat preference, water consumption, and drinking frequency in 2004 during the summer when water consumption might be a limiting factor. The trial consisted of two stages. First, we placed graduated buckets of water (15 L) in the middle of smoothed round sandy arenas (1 m radius) located at the far corner of each of the two habitats (a distance of ~400 m apart) for 15 days. Since the deer selected a different patch every day rather than traveling long distances in the study site (Wallach 2005), we were able to determine which habitat was preferred, based on the habitat in which they were sited each day, and the difference between the amounts of water consumed in each habitat. Second, we removed the water source from the preferred habitat and left a water source only in the nonpreferred habitat for an additional 16 days.

The drinking frequency was not determined by direct observations, but rather by counting the number of tracks a single doe left in the sandy arena surrounding the water bucket and then relating it to the amount of water she consumed in a single drinking event (track index and water index, respectively). The number of tracks the deer left on the sand and their water consumption in a single drinking event were initially repeatedly measured by direct observation until reliable indices were achieved. These indices were used later to estimate drinking frequency by dividing the number of tracks found and the amount of water consumed by these index numbers (Fig. 1).

Statistical analysis

We compared WTO and DEE between seasons using a Student's t test, since only three does were measured in winter and all four does were measured in summer. Water consumption was compared between seasons and between habitats using paired t tests. When the water consumptions of all four does were measured together, each day was treated as a replicate. To analyze the relationship between season and water consumption, we ran a Kruskal–Wallis nonparametric test (nonhomogenous data). Exponential correlation was used to characterize the relationship between temperature and water consumption. We determined habitat preference with a combined probability χ^2 test. Repeated-measures ANOVA was used to determine the difference between water consumption in the two habitats. A Student's t test was used to determine whether habitat preference affected drinking frequency. All tests were considered significant at $P < 0.05$ and were carried out with SPSS® for Windows® version 13 (SPSS Inc. 2004).

Results

WTO and dietary and free-water consumption

DEE in the winter was not significantly different from summer (5196 ± 1069 vs. 5101 ± 1397 kJ/day, respectively: $t = 0.27$, df = 5, $P > 0.05$). WTO was significantly higher in the winter (3.3 ± 0.3 L/day) than in the summer (2.1 ± 0.2 L/day) ($t = 6.63$, df = 5, $P < 0.01$). Percent body water was slightly higher in the winter (74%) than in the summer (70%), but the difference was not statistically significant ($t = 1.24$, df = 5, $P > 0.05$).

The observations over a 24 h period revealed that the deer were active similarly in the winter (47% of the day) and in the summer (48% of the day), but they spent 8.4 h actively feeding in the winter and only 6.1 h in the summer (paired $t = 8.187$, df = 3, $P < 0.01$). In both seasons, the deer were most active during dawn and dusk. During the observations in the winter, not a single drinking event was recorded. In the summer, of the 52 drinking events that were observed, the majority took place between 0630–0830 and between 1500–1930 (Fig. 2).

The deer consumed ~3 kg/day of food from which they obtained a daily average of 2 L of H_2O in the winter in both habitats. In the summer, we found that the deer obtained significantly more water from their diet in the mature habitat (0.5 ± 0.04 L of H_2O daily) compared with in the young habitat (0.3 ± 0.03 L of H_2O daily) (paired $t = 7.72$, df = 3, $P < 0.01$), even though free water ($t = 0.61$, df = 13, $P > 0.05$) and food consumption (paired t test, $t = 0.44$, df = 3, $P > 0.05$) did not differ. Their food contained $56.62\% \pm 0.03\%$ water in the winter, but only $20.88\% \pm 0.03\%$ water in the summer. The deer gained additional metabolic water from the consumed food (≤171 and ≤128 mL/day in the winter and summer, respectively).

Free-water consumption was highest in the summer and lowest in the winter (Kruskal–Wallis, $H = 41.59$, df = 3, $P < 0.0001$), and was inversely related to precipitation (Fig. 3). The free-water consumption measured for each doe individually during the summer (2 ± 0.2 L/day) was higher than the mean free-water consumption measured for the four does together (1.6 L/day per deer; Fig. 3). We consider this latter value to be more reliable because of the larger number of replicates ($n = 15$). Throughout the year, water consumption was highly correlated with temperature ($y = (5 \times 10^{-7})x^{4.53}$, $R^2 = 0.67$, $P < 0.001$). Water consumption increased exponentially in relation to temperature and most dramatically when temperatures were higher than ~22 °C (Fig. 4); however, within season, temperature fluctuations had no significant effect on water consumption except in the spring ($y = (4 \times 10^{-6})x^{3.88}$, $R^2 = 0.429$, $P < 0.01$). Overall, the amount of the three water sources (free, preformed, and metabolic waters) added up to the value of WTO in the summer, with free water as the dominant source (76%, Fig. 5a). In contrast, preformed water provided the majority of the WTO of the does in the winter, but 23% (~0.7 L/day) of their WTO was not accounted for (Fig. 5b). Nevertheless, the deer did not lose mass in either season.

Water consumption in different habitats

When water sources were placed in both habitats, we

Fig. 1. An example of track (*a*) and water (*b*) indices established for each trial by observing a European roe deer (*Capreolus capreolus*) during drinking events. Here the deer left ~8 tracks on the sand and consumed 0.7 L during a single drinking event.
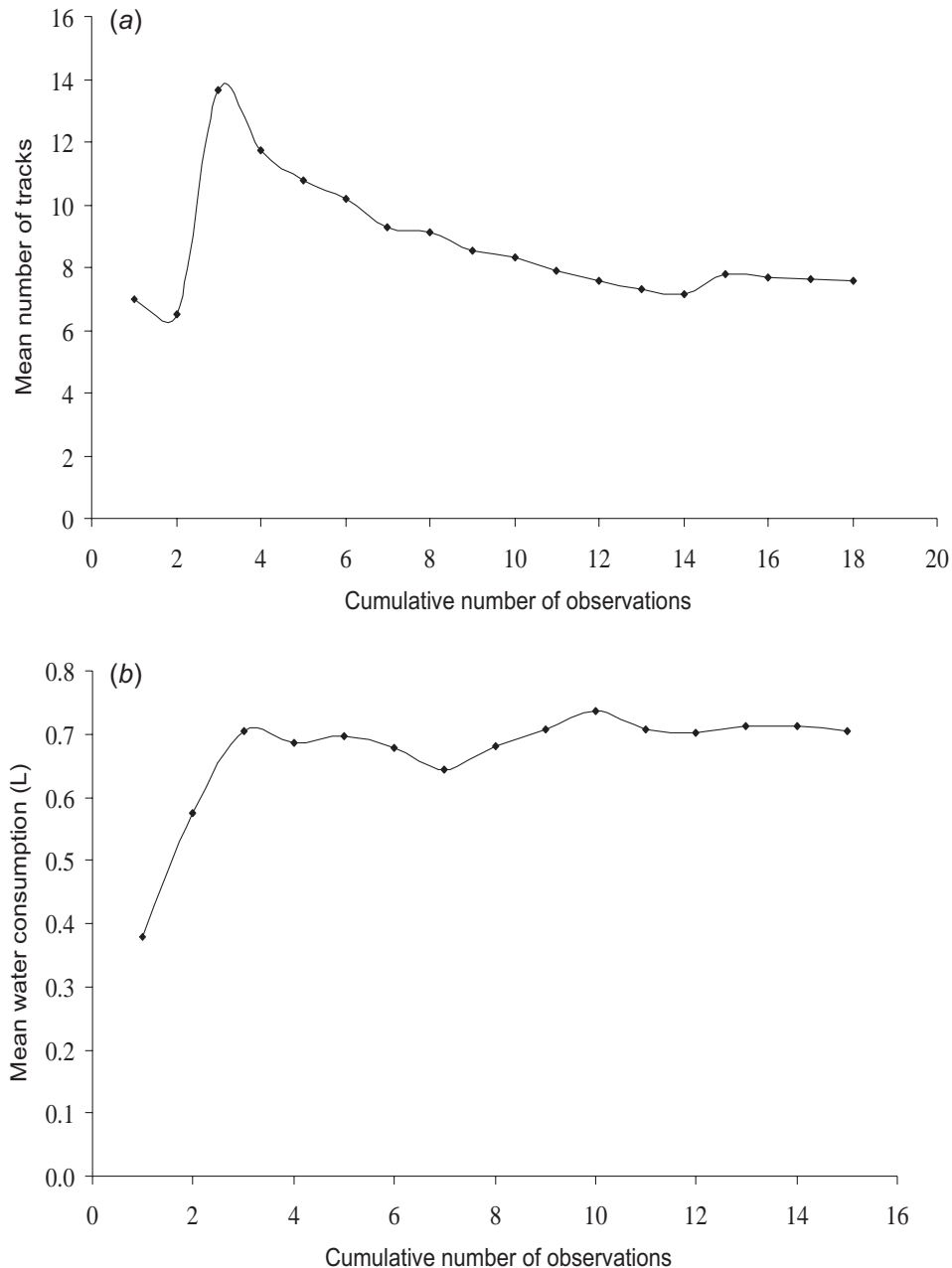
sighted the deer significantly more in the mature habitat (combined probability χ^2, $P < 0.01$), which also had significantly more drinking events (repeated-measures ANOVA, $F_{[10,21]} = 12.97$, $P < 0.01$). Therefore, in our experimental system, the mature habitat was defined as the preferred habitat. When the water source was provided only in the young (nonpreferred) habitat, the deer maintained their preference for the mature habitat (combined probability χ^2, $P < 0.05$). Daily free-water consumption did not change between the two habitats, with each deer drinking ~1.4 ± 0.3 L/day ($t = 0.3$, df = 17, $P > 0.05$). However, we did observe a change in drinking frequency. When water was available in the pre-

ferred habitat, the drinking frequency of the deer was significantly higher (Table 1).

Behavioral observations during the drinking events suggested that the deer were stressed after 24 h without drinking. They ran and fought for access to the water source, and prevented an inferior doe from approaching the water. These behaviors were only observed when the water source was restricted to the nonpreferred habitat. In addition, in this latter location, they drank their entire daily water intake in one bout (1.4 L in 3 min), which was followed several times by vomiting. After ~24 h without drinking, the deer lost 5.3% ± 1.0% of their body mass (range 3.3%–8.5%).

Fig. 2. Percentage (mean + SE) of drinking events (out of 13 ± 2 drinking events) by a single European roe deer observed at half-hour intervals for six 24 h periods during the summer.
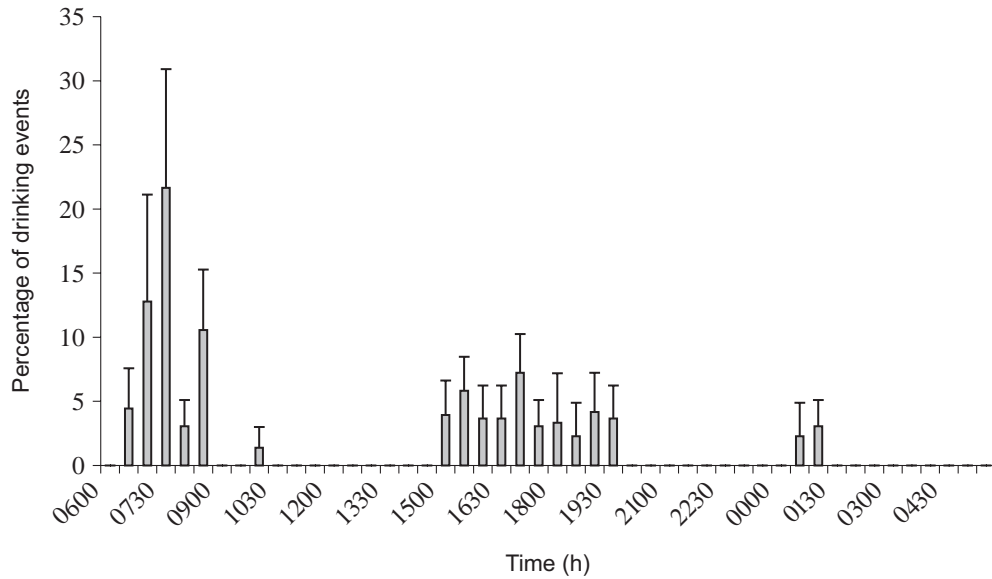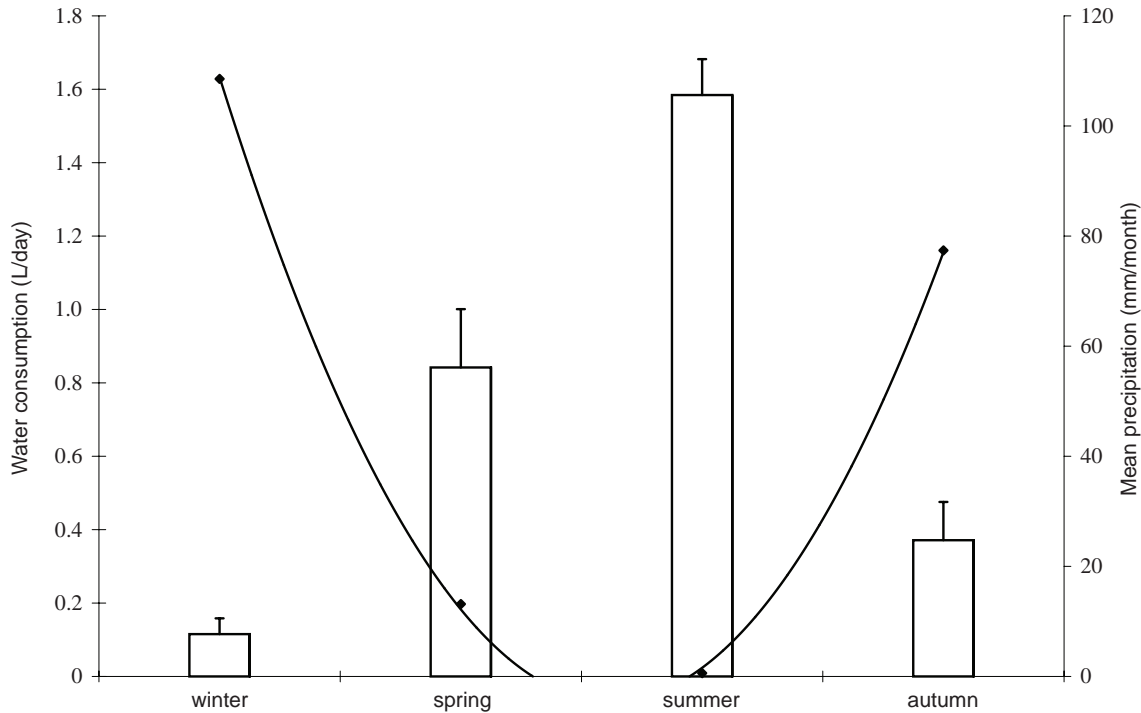

Fig. 3. Daily water consumption (mean + SE) by four nonlactating European roe deer does in a dry Mediterranean forest (bars) and the mean precipitation during each season (line; precipitation data available from http://cbs.gov.il [accessed 28 December 2004]).

Discussion

Water availability as a physiological constraint

Studies of the roe deer at the northern edge of its distribution during harsh winters have demonstrated that the WTO of the roe deer can change according to diet and temperature (Holand et al. 1998). In the present study, we assessed the WTO of the roe deer at the southern edge of their distribution, where summer is the harsh season. We found that roe deer have a higher WTO in the winter (winter–spring) than in the summer (summer–autumn) despite the constant availability of free water.

Williams et al. (2001) examined water influx rates of the Arabian oryx, which is a desert-adapted ungulate that does not need to drink free water. They used a DLW technique to study WTO on free-ranging animals during the hot and dry summer and during the moist and mildly cool spring of Saudi Arabia. Similar to our findings with roe deer, the Arabian oryx was shown to have a lower rate of water influx in the summer (1.3 L/day) than in the spring (3.4 L/day). How-

Fig. 4. Daily water consumption by European roe deer in a Mediterranean environment increases exponentially as temperatures rise throughout the year.
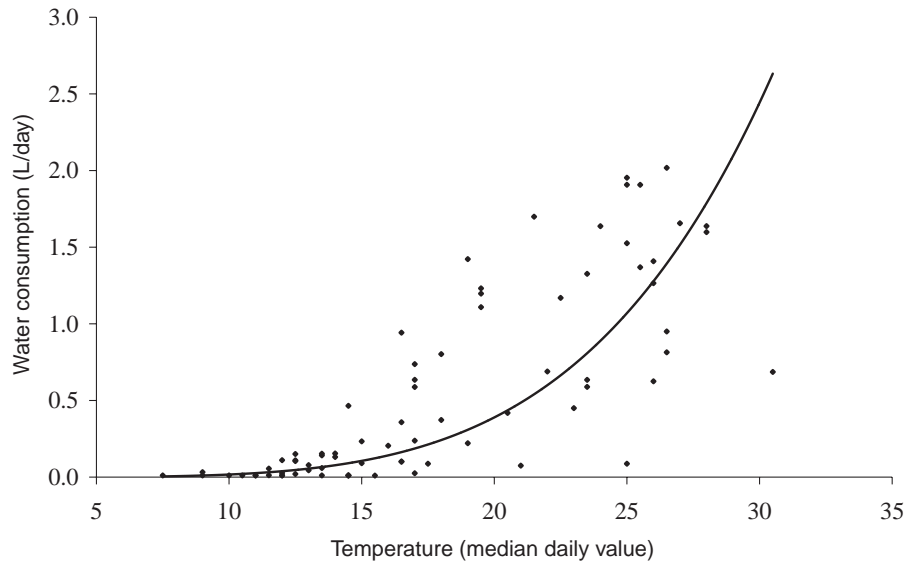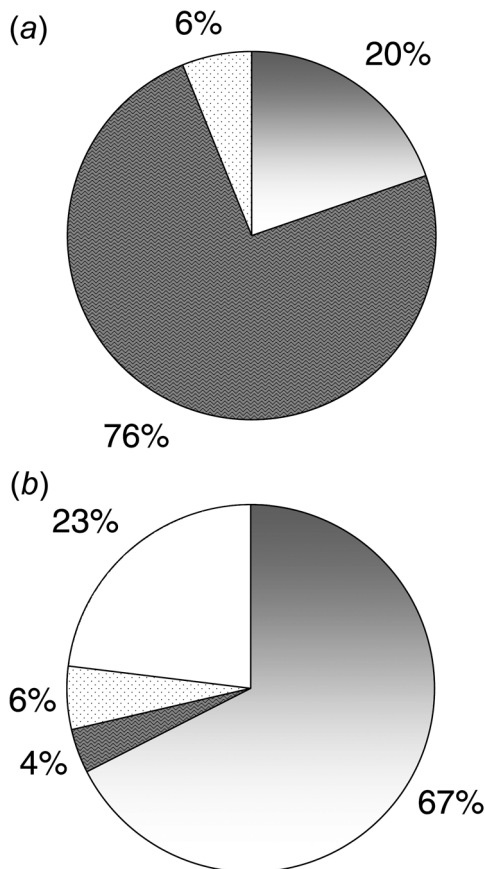

Fig. 5. Percentages of water turnovers in European roe deer obtained from their diets (shaded), free water (jagged lines), metabolic water (dotted), and unknown (open) during the summer (*a*) and winter (*b*).

economy is inferior to desert ungulates, but resembles that of mesic deer. For example, the Sitka black-tailed deer (*Odocoileus hemionus sitkensis* Merriam, 1898) in Alaska exhibits water transfer rates that are four times higher during the productive season (summer) than during the cold and unproductive season (Parker et al. 1993).

Comparisons of DEE values from this study with allometric predictions for similarly sized free-ranging eutherians showed that winter and summer values were, respectively, 30% and 38% less than the prediction of Nagy et al. (1999) for mammals, 16% and 25% less than the prediction of Anderson and Jetz (2005), and 7% greater and 3% less than the prediction of Speakman (2000; eq. 2). Interestingly, we have found that WTO changed between seasons despite having a similar DEE. For comparison, the Arabian oryx exhibits a decrease of energy expenditure of the same magnitude as the WTO from the spring to the summer (Williams et al. 2001). The lack of variation in DEE between summer and winter, found in this study, is in agreement with Mauget et al. (1997*a*, 1997*b*), who concluded that roe deer do not have an endogenous seasonal metabolic rhythm. Since the variation in WTO depends largely on the metabolic rate of the animal (Nagy and Peterson 1988), our results suggest that the roe deer possess some degree of physiological adaptation to water-restricted habitats which does not affect their metabolic rate.

In the winter, the deer obtained the majority of their water requirement from vegetation. We found a large discrepancy (23%) between their overall water consumption and their WTO in the winter, although water is not a limiting factor during this season and they did not lose mass. This may be explained by the larger variation in water content of vegetation in winter than in summer. In the summer, the pattern was reversed; the deer obtained three quarters of their water from drinking. Although WTO of nonlactating does was shown to be lower in the summer than in the winter, it made up 8% of their body mass. A comparable amount of water extracted from leaves will require the deer to consume an unrealistic amount of food (8 kg) each day, which is

ever, when comparing these results relative to body mass (the oryx weighed ~85kg), the WTO of the Arabian oryx was only 17%–28% of the WTO of the roe deer. Thus, although roe deer show flexibility in WTO, their water

Table 1. Daily drinking frequency of European roe deer (*Capreolus capreolus*) when the water source was available in a preferred habitat (i.e., mature forest) and restricted to a nonpreferred habitat (i.e., young forest).

	Preferred habitat (mean ± SE)	Nonpreferred habitat (mean ± SE)	t	P
Water index	2.0±0.2	1.4±0.2	2.40	<0.05
Track index	1.8±0.3	1.4±0.3	1.08	>0.05

~35% of the body mass. Metabolic water accounted for only 6% of their water consumption.

Within season, temperature fluctuations had no significant effect on water consumption, apart from spring, presumably because variability within seasons is too small to detect an effect at this sample size. However, throughout the year, water consumption increased exponentially relative to temperature, especially most dramatically when temperatures were higher than ~22 °C (Fig. 4). This result, along with global warming, should be taken into consideration in future management of roe deer, especially around the Mediterranean basin where drought stress is expected to increase (Thuiller 2007).

In Mediterranean regions, roe deer prefer areas that include a source of open water (Tellería and Virgós 1997), and they have a preference for more moist habitats (Virgós and Tellería 1998, but see Gerard et al. 1997). Indeed, rainfall was the best predictor of roe deer densities in central Spain (Sáez-Royuela and Tellería 1991). Sáez-Royuela and Tellería (1991) proposed that the low density of roe deer in the Mediterranean region is explained by rainfall acting as a limiting factor on vegetative productivity, and consequently, on the carrying capacity of the region. The results of this study suggest that free water constrains roe deer distribution.

As the data were obtained from nonlactating does, it is expected that lactating does would require an excessive amount of free water (Parker et al. 1993; Degen 1997). The water needs of a mammalian female may increase by ~50% or more during lactation (Degen 1997). The milk consumption of our bottle-reared fawns peaked during July (0.7–0.8 L/day per fawn; Wallach et al. 2007), which is the hottest and driest time of the year in Israel. Therefore, it is expected that a female with 2–3 fawns would require more than the observed 2 L/day. These results emphasize a critical demand for an adequate water supply for roe deer in dry Mediterranean habitats. It can be argued that captive animals, accustomed to having unlimited access to water, do not tolerate water deprivation as well as wild-born animals. Tatwany and Goldspink (1996) found that despite wild mountain gazelles surviving without free water in Saudi Arabia, gazelles that were bred in captivity and had access to free water could not survive without it. Therefore, it is possible that the reintroduced population would be more resilient to water deprivation after several generations in the wild. In addition, this study is based on only four hand-reared animals, and therefore should be regarded as a first attempt at exploring this subject.

The importance of the location of the water source

When the water source was placed in a nonpreferred habitat (young habitat), the deer significantly reduced their vis-

its to the water source and appeared to be very thirsty. Despite the short distance (400 m) from the preferred (mature) habitat, they did not change habitats in response to the change in the location of the free-water source; rather, they made quick and infrequent excursions to the water source, while drinking more at each visit. Nonlactating white-tailed deer also drink once or twice per day depending on the location of the water source, but a lactating white-tailed deer might need to drink more often (Hiller 1996). Potentially, the released deer would also move out of their preferred habitat to reach water sources. However, in the hot climate of the eastern Mediterranean, this behavior may impose additional physiological stress upon the deer, especially on lactating does.

Sociality might also affect the water consumption of roe deer. The white-tailed deer, which has an ecological niche that is similar to that of the roe deer (Putman and Moore 1998), is reliant on access to free water (Lautier et al. 1988). Therefore, water sources are usually found in the center of its range (Hiller 1996). When there is a shortage of water, white-tailed deer tend to gather in areas where water is available (Hiller 1996). Bowyer et al. (2001) found that 77% of mule deer occurred within 500 m of a free-water source in a Mediterranean-like region of California. However, roe deer are territorial (males during spring and summer) and solitary, and females actively defend kidding sites (Andersen et al. 1998). Potential conflicts between territorial individuals over water sources in xeric habitats should be investigated further.

Management recommendations

Under dry Mediterranean environments, availability of free water in the summer is both a physiological contraint and a behavioral constraint for roe deer. Apart from the critical demand to drink, the location and distribution of water sources in the release site should affect the reintroduction success. Because of the strong association of roe deer with woodland structures (Andersen et al. 1998), it is important that potential release sites should contain free-water sources that are located in dense forest areas. The solitary and territorial natures of roe deer prescribe that the water sources should be scattered throughout their range. Lack of water in the release site may increase the attractiveness of irrigated agricultural fields, thus increasing potential conflict with farmers.

This study demonstrates the importance of feasibility studies in reintroduction programs at the edge of a species range. As global climatic warming and human demands cause a decrease in free-water availability, especially in water-limited ecosystems such as the eastern Mediterranean forest, we recommend that the availability of this resource be taken into consideration in management decisions. In ad-

dition, we recommend a combined physiological and behavioral approach in determining the ecological requirements of a species.

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