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Interactions between Green Turtles (*Chelonia mydas*) and Foxes (*Vulpes vulpes arabica*, *V. rueppellii sabaea*, and *V. cana*) on Turtle Nesting Grounds in the Northwestern Indian Ocean: Impacts of the Fox Community on the Behavior of Nesting Sea Turtles at the Ras Al Hadd Turtle Reserve, Oman

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Vanda Mariyam Mendonça, Salim Al Saady, Ali Al Kiyumi, and Karim Erzini (2010) Interactions between green turtles (*Chelonia mydas*) and foxes (*Vulpes vulpes arabica*, *V. rueppellii sabaea*, and *V. cana*) on turtle nesting grounds in the northwestern Indian Ocean: impacts of the fox community on the behavior of nesting sea turtles at the Ras Al Hadd Turtle Reserve, Oman. *Zoological Studies* **49**(4): 437-452. Green turtles *Chelonia mydas* nest year round at the Ras Al Hadd Nature Reserve, Oman, with a distinct lower-density nesting season from Oct. to May, and a higher-density nesting season from June to Sept. On these beaches, the main predators of turtle eggs and hatchlings are foxes *Vulpes* spp., wolves *Canis lupus arabs*, and wild cats *Felis* spp. and *Caracal caracal schmitzi*. During 1999-2001, both the nesting behavior of these turtles and the diets of foxes (the main predator on the beaches) were investigated, and we tested whether female turtles were able to avoid/reduce predation pressure on their eggs and hatchlings on the nesting grounds. Elsewhere in the region and globally, foxes are known to feed on rodents, lizards, birds, and insects, but at Ras Al Hadd, their diet is basically composed of sea turtle eggs and hatchlings (comprising about 95% in volume), with smaller contributions from other marine invertebrates (mostly ghost crabs *Ocypode* spp. and large gastropods), although they also sporadically ingested birds and lizards. The ability to adapt to a diet of sea turtle eggs and hatchlings, on these beaches, is certainly a factor behind the success of this carnivore community in the arid lands of the Arabian Peninsula. Field experiments indicated that nesting sea turtles recognized both natural predators and humans as threats to their offspring, and this was reflected in modifications to their nesting behavior. In relatively undisturbed areas (by both natural predators and humans), sea turtle nest density was significantly higher, and nests were placed further away from the surf's edge, in contrast to results from relatively disturbed areas, where turtle nests were closer to the surf's edge, thus reducing the distance hatchlings had to travel when they emerge and begin their journey to the sea. Nesting turtles interrupted their nesting cycle if they sensed the presence of people or foxes, returning to the sea without laying a clutch. However, if they had already initiated oviposition when they sensed the presence of people and/or predators, they continued, although they significantly increased efforts to camouflage their nests. Other reasons behind nest site abandonment included sand collapsing events (critical during preparation of the egg chamber) and intraspecific competition for nest sites. These behavioral patterns of sea turtles result from their evolutionary adaptation to nesting on beaches, which surely played a role in their survival, but also highlight the importance of minimizing human disturbance and activities on turtle nesting beaches. http://zoolstud.sinica.edu.tw/Journals/49.4/437.pdf

Key words: *Chelonia mydas*, Ras Al Hadd, *Vulpes cana*, *Vulpes rueppellii sabaea*, *Vulpes vulpes arabica*.

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Predator avoidance behavior has been observed in several species (e.g., Nelson 2007), and predation pressure has affected sea turtle populations throughout their evolution; with both prey and predators adapting to coexist and survive. Stancyk (1995) referred to the nocturnal nesting, production of large numbers of eggs in multiple clutches per season, elaborate nest concealment, and nocturnal hatchling emergence as just some adaptations to predation. However, previous studies on interactions between nesting sea turtles and their predators, such as terrestrial mammals, are virtually nonexistent.

Green turtles *Chelonia mydas* (Fig. 1) nest all year round at the Ras Al Hadd Nature Reserve, Arabian Sea (Ross and Barwani 1982), with 2 distinct nesting seasons throughout the year: a higher-density nesting season from June to Sept. and a lower-density nesting season from Oct. to May. This pattern is unlike that of any other sea turtle population worldwide, with exception of the green turtles nesting off the Pakistani coast, Gulf of Oman (Asrar 1999), and may also occur with green turtles nesting on the Hadramawt coast off Yemen, Gulf of Aden. According to governmental authorities in charge of the management of Ras Al Hadd protected area, during the 1990s, at least 15,000 female green turtles annually nested at the Ras Al Hadd Nature Reserve, on the many beaches on the 42-km-long coastline. The high number of turtles coming to nest at Ras Al Hadd makes this rookery amongst the most important sea turtle rookeries worldwide. According to the local authorities, over the same period, mortality by incidental capture in fishing nets of adult green turtles at Ras Al Hadd was 37 ind./yr, and the female: male ratio of stranded carcasses was 2: 1. Mortality rates are especially high in the area, most likely due to the number of fishing vessels operating in the highly productive Arabian Sea, and also because of the intense maritime traffic in this oil-rich region (Mendonça et al. 2004). Salm (1991) suggested a mortality rate of 1,000-6,000 individuals (ind.)/yr, and Sideek and Baldwin (1996), using those numbers, assessed the Oman green turtle stock using a stage-class matrix model. Although all sea turtles (Chelonidae and Dermochelidae) are listed as endangered species locally and globally (e.g., IUCN 2008), harvesting turtles for meat is still a common practice among fishermen in the region.

Fig. 1. A juvenile green turtle *Chelonia mydas* photographed in 2003 in one of the coastal lagoons (khawrs) of the Ras Al Hadd Turtle Reserve, Oman.

On the other hand, on nesting grounds, the predation pressure on sea turtle eggs and hatchlings by terrestrial mammals such as the Arabian grey wolf *Canis lupus arabs* and foxes *Vulpes* spp., is a serious factor affecting the survival of this sea turtle population. Here, both marine and terrestrial species are part of the same complex food web, with the fox community unexpectedly playing a major role in intertidal and supralittoral areas. Preventing predation of sea turtle eggs and hatchlings by terrestrial carnivores is not an alternative, as these mammal populations are regionally endemic and also in need of protection (e.g., Larivière and Seddon 2001, Sillero-Zubiri et al. 2004, Drew and Torenq 2005, Drew et al. 2005). Even relatively abundant species such as the Arabian red fox *Vulpes vulpes arabica* are subjected to high mortality rates due to relatively frequent outbreaks of rabies, which also affect the endangered Arabian grey wolf *C. lupus arabs* (Al Ismaily and Al Mauly 1996).

At the Ras Al Hadd sea turtle nesting grounds, the fox community is the main cause of mortality of sea turtle eggs and hatchlings. As observed from several studies on predator-prey interactions although in ecosystems involving other prey and other predators (e.g., Mendonça et al. 2007a b 2009), predation pressure may significantly affect the prey community density and structure. In the present study, a series of experiments was conducted at the Ras Al Hadd Nature Reserve, to test whether nesting female green turtles *C. mydas* are able to display any changes in their nesting behavior in order to avoid or reduce mortality to their offspring.

MATERIALS AND METHODS

The study site: Ras Al Hadd Nature Reserve

The Ras Al Hadd Nature Reserve, in Oman, covers an area of 120 km^2, including sandy beaches, sand dunes, sabkha (hypersaline coastal plains characteristic of the Arabian Peninsula), limestone mountains and cliffs, Early Tertiary coastal plains, and Hawasina mountains (of marine sediments from the Middle Permian to Cretaceous; Hanna 1995). The reserve also includes 2 khawrs (Khawr Al Hajar and Khawr Al Jaramah; coastal lagoons characteristic of the Arabian Peninsula), supporting black mangrove *Avicenna marina* forests (JICA 2004).

The sandy beaches at Ras Al Hadd provide nesting grounds for sea turtles and habitat for regionally endemic terrestrial mammals. Green turtles *C. mydas* are the only sea turtle species nesting in the area, although hawksbill turtles *Eretmochelys imbricata* are also observed feeding in the offshore coral reefs dominated by *Acropora* spp. and *Porites* sp. (Mendonça et al. 2010). The coastline also provides important grounds (nesting, feeding, and resting) for many bird species. According to Eriksen (1998), the list of confirmed species breeding at Ras Al Hadd includes Striated Herons *Butorides striatus* and the Brown-necked Raven *Corvus ruficolis*. The offshore areas also have algal mats dominated by *Padina* spp. and *Ulva* spp. (Mendonça et al. 2010), and seasonal floating seagrass beds of *Sargassum* spp. limited to the summer monsoon (Jupp et al. 1996). In addition, several cetacean species have been sighted off Ras Al Hadd cape, including the common dolphin *Tursiops truncatus* and dwarf whale *Kogia simus* (OCRG 2004).

The 2 main turtle nesting areas within the Ras Al Hadd Turtle Reserve are 2 Ras Al Jinz beaches, near the Ras Al Jinz fishing village, and Ras Al Hadd Beach at the town of Ras Al Hadd. The Ras Al Jinz area had a permanent camp area for tourists from 1991 to 2008, set up by governmental authorities, which provided guided visits (average, 9,483; range, 3,631-16,814 ind./yr) by park rangers to one of the beaches. After reforms in the authority in charge of the nature reserve, the rangers limited their role to patrolling the beaches, while the newly created Ras Al Jinz Scientific and Visitor Centre now caters to visitors. Visitors are only allowed onto the northern Ras Al Jinz Beach, while the southern Ras Al Jinz Beach was left undisturbed by tourists, although fishermen from the nearby Ras Al Jinz Village still keep their boats and fishing gear on the far-southern corner.

The present study was conducted at the southern Ras Al Jinz Beach, a sandy beach flanked on both the northern and southern extremes by limestone cliffs with many caves at the intertidal level, and also on the supralittoral. The caves are inhabited by terrestrial carnivores such as foxes *Vulpes* spp. and cats *Felis* spp. There are no previous studies on these populations, their diets, or their unequivocal ecological roles in this coastal ecosystem. The only available studies on foxes in Oman are on Rüppell's fox *V. rueppellii sabaea* in inland areas of the nearby Wahiba Sands desert, about 200 km south of Ras Al Hadd (Linn 1988), and in the Jiddat Al Harasis, about 500 km south of Ras Al Hadd (Lindsay and MacDonald 1986). More recently, Spalton (2002) in a review on the Canidae in Oman added his observations also in inland areas.

Predators of turtle eggs and hatchlings and their diets

In order to identify and quantify the abundance of potential predators of sea turtle eggs and hatchlings, Ras Al Jinz beaches and the surrounding area (up to 2 km inland) were covered by foot, along several transects, in both summer (during the higher-density nesting season for sea turtles) and autumn (during the lower-density nesting season for sea turtles), during 1999-2001 and again in 2009. For the most abundant crab species *Ocypode* spp., crab holes were counted in 10 quadrates (of 3 × 3 m) randomly placed on the supralittoral. No crab holes were identified on the intertidal, although most individuals were observed on the intertidal. Observations of birds were also conducted during both seasons, and during high- and low-tidal conditions in order to obtain a number which would be more representative of the population at the Ras Al Jinz beaches. Abundances were converted into ind./km/yr. For terrestrials mammals, abundance was based on sightings, footprints, and feces, and standardized per units of area (ind./km^2), using a logarithmic scale (0-1, 1-10, 10-100, and 100-1000), as it was difficult to attribute exact numbers to populations with individuals moving over a relatively large area.

As foxes (Arabian red fox *V. v. arabica*, Rüppell's sand fox *V. rueppellii sabaea*, and Blandfor's fox *V. cana*) revealed themselves as the most important predator population on turtle nesting beaches at Ras Al Jinz, their diets were studied from direct observations of foxes hunting and feeding, by analyzing food stored by foxes on the bare-ground area behind the beaches, and from scat analyses. Direct observations of fox activities took place in both June and Oct. 2000 (*n* = 20 foxes per season), and in May-June 2009, during full-moon nights, as the visibility on other nights was very reduced. Observations of food stored by foxes, and later excavated by foxes, and left re-exposed (*n* = 20 near the intertidal caves and *n* = 20 near the supralittoral caves, about 1 km inland) took place at Ras Al Jinz, and at 2 other sites within the Ras Al Hadd Turtle Reserve, north of Ras Al Jinz. Areas with caves were visited during the daytime. At each site, 20 droppings were collected for analysis, and at least 20 re-exposed storage areas were investigated. Diets (percentage of prey items in the fox diets) between the 3 fox species were not compared as it was not always clear which of the 3 species we were dealing with. Results from re-exposed stored food and scat analyses, between seasons in 2000 at Ras Al Jinz, and between sites were compared by an analysis of variance (ANOVA) after arcsine-data transformation, as this ensured the normality of the data. The probability (*p*) level of significance was estimated using the Bonferroni test (Sokal and Rohlf 1995).

Nesting sea turtles on Ras Al Jinz beaches

The studied turtle population of *C. mydas* (eggs, hatchlings, and adult females) was measured using standard methods (e.g., Eckert et al. 1999). Adults were sampled when returning to the sea after nesting or attempting to nest, and emerged hatchlings were also intercepted for measurements on their way to the sea. In adults, the curved carapace length (CCL, *n* = 36), curved carapace width (CCW, *n* = 36), plastron length (PL, *n* = 7), tail length from cloaca to tail end (TL, *n* = 7), and weight (W, *n* = 7, using a dynamometer) were recorded. For hatchlings, only the CCL (*n* = 17) and CCW (*n* = 17) were recorded. Three clutches were sampled for clutch size and egg diameter (5 eggs per clutch), and the percentage of non-fertilized eggs was also recorded. Finally, the mean size of the nests (body chamber maximum length, width, and depth) was recorded (*n* = 19).

Sea turtles have 8 behavioral phases during the nesting process on beaches (e.g., Hendrickson 1995): ascending from the sea to the beach (phase 1, from water to the surf's edge); wandering (phase 2, from the surf's edge to the 1st movement of a front flipper to begin digging the body pit of a nest); digging the body chamber (phase 3, from the 1st movement of a front flipper to begin digging the nest until the 1st movement of a rear flipper to begin digging an egg chamber); digging the egg chamber (phase 4, from the 1st movement of a rear flipper to begin digging an egg chamber until the turtle begins laying eggs); oviposition (phase 5, turtle immobilized and laying eggs); filling the egg chamber (phase 6, from the 1st movement of a rear flipper to begin filling the egg chamber with sand until the 1st movement with a front flipper to begin filling the body chamber with sand); filling the body chamber and camouflaging the nest (phase 7, from the 1st movement with a front flipper to the moment when the turtle leaves the nest site; this phase in our study included camouflaging, as we could not distinguish the moment when turtles finished covering the body pit and began camouflaging it); and return to the sea (phase 8, movement from the nest site to the sea). The duration of each of these phases was recorded for green turtles *C. mydas* nesting at the southern Ras Al Jinz Beach in June 2000. The duration of each nesting phase was compared among individual turtles by ANOVA (e.g., Sokal and Rohlf 1995). The sample size was 13 < *n* < 27 ind., depending on the nesting phase, as some turtles did not complete the nesting process.

While performing the above 8 nesting phases, sea turtles undergo exercise-rest cycles, which include 1 interval of exercise and 1 interval of rest, usually lasting < 1 min for the whole cycle. The duration of the exercise-rest cycles (exercise interval + rest interval) of nesting sea turtles *C. mydas* at the southern Ras Al Jinz grounds was also measured during the 8 nesting phases. Exercise-rest cycles were studied for 4 individual green turtles in Oct. 2000, during the lower-density nesting season. The observer stood about 20-30 cm behind the turtle with a stopwatch, and the duration of each exercise-rest cycle was recorded. Occasionally, a turtle did not complete the entire phase because of unfavorable conditions. Exercise-rest cycles were compared by ANOVA for each of the nesting phases. The oviposition phase was excluded from this study because of the minimal activities during this phase. The observed nesting behavior did not take into consideration if the presence of terrestrial mammals played a role in the displayed variation of the results.

Impacts of the fox community

Three experiments were conducted at the southern Ras Al Jinz Beach to test whether sea turtles react to the presence of predators, and whether they are able to display any mechanism and/or strategies to avoid or reduce predation pressure on their eggs and hatchlings. Experiments were conducted throughout the year at low-tide conditions and during full-moon nights, providing the best visibility conditions for night observations, but this also required that observers avoid being seen by the turtles.

Experiment 1: Testing predator avoidance when choosing a nest site. In order to investigate if nest abundance and placement were affected by disturbances by either humans or natural predators, nest site abundance and placement were recorded daily during 5 consecutive days in autumn 2000, on 3 selected sections of the southern Ras Al Jinz Beach (Fig. 2): section 1 was an area highly disturbed by fishermen (where they keep fishing boats and gear); section 2 was clearly less disturbed, by both fishermen and natural predators; and section 3, closer to the cliffs with caves was very disturbed by natural predators, especially red foxes *V. v. arabica*. In each section, 5 areas of 10 m width (parallel to the shoreline) and 70 m inland were surveyed. Nests were counted, and the distance to the surf's edge

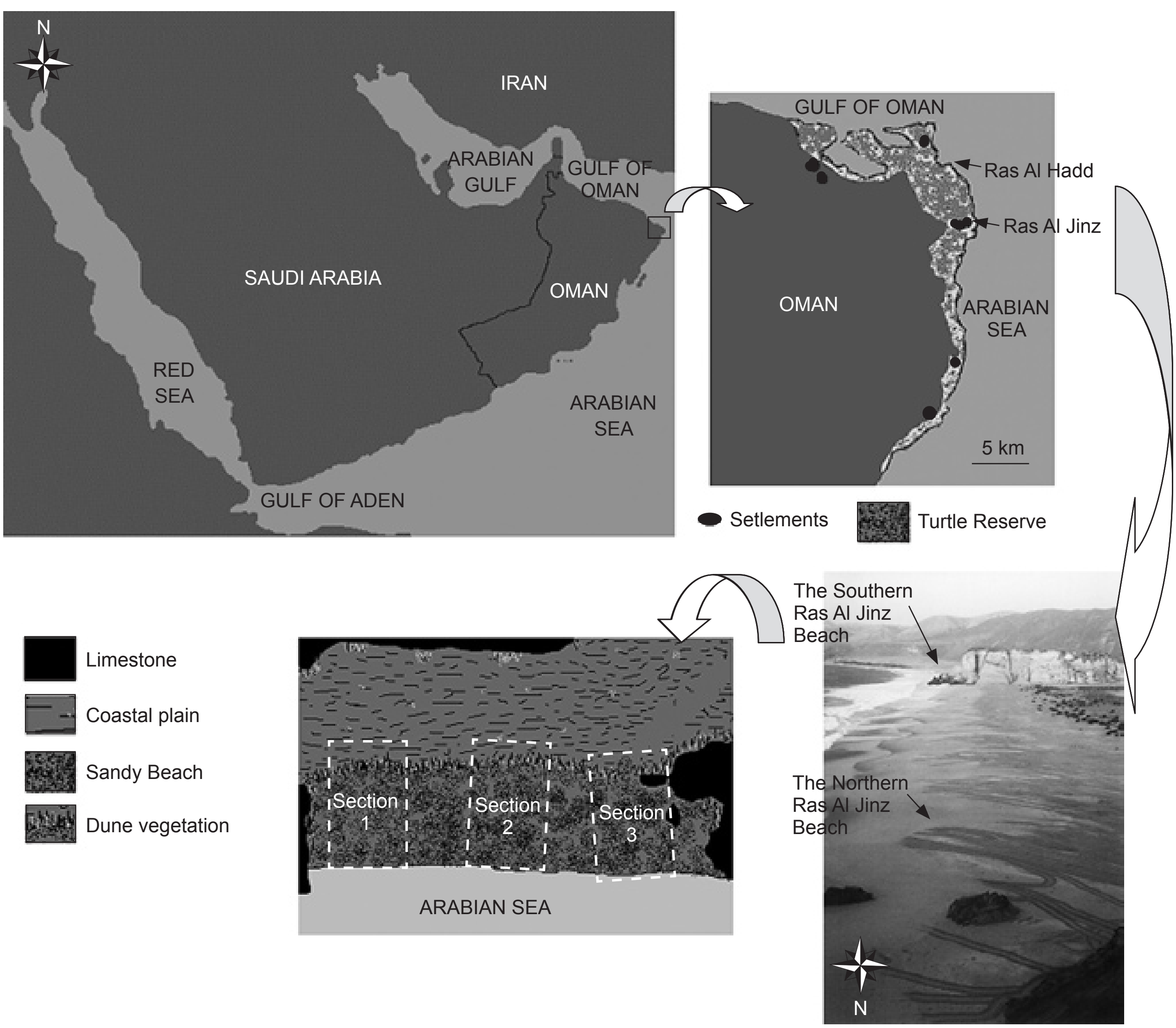

Fig. 2. The Ras Al Hadd Turtle Reserve in Oman. At the Southern Ras Al Jinz Beach, Ras Al Hadd Reserve, 3 sections were considered to test the impacts of the fox community on the sea turtle population. Section 1 was particularly disturbed by fishermen; section 2 was relatively undisturbed by both fishermen and natural predators; and section 3 was particularly disturbed by foxes.

recorded. Both nest abundance and placement per section were compared among the 3 sections, and between the sampled days (for each section) by ANOVA; the probability (p) level of significance was determined by the Bonferroni test (Sokal and Rohlf 1995).

Experiment 2: Testing predator avoidance after choosing a nest site. In order to investigate if the behavior of nesting females was affected by disturbances by natural predators and humans, 2 treatments were considered to study the duration of nesting phases: in the presence and absence of foxes, mostly *V. v. arabica* (treatment 1 and control 1, respectively) and in presence and absence of people (treatment 2 and control 2, respectively). For each treatment and for each respective control, the behavior of 10 turtles was recorded. The duration of each nesting phase was also compared between treatments by ANOVA.

Experiment 3: Testing if nest abandonment before turtles began laying their eggs was related to predator disturbance

In order to investigate the reasons for nest site abandonment before oviposition, and whether natural predators and human presence may be behind this, the behavior of 64 nesting female turtles (n = 32 in summer during the higher-density nesting season and n = 32 in autumn during the lower-density nesting season) was studied. The percentage of turtles completing the nesting process, the percentage of those abandoning the nesting process, and the reasons for nest site abandonment were recorded.

RESULTS

Nesting sea turtles at Ras Al Jinz

Sampled female green turtles presented the following morphometrics: a mean CCL of 102.75 cm, a mean CCW of 92.86 cm, a mean PL of 79.28 cm, and a mean TL of 7.57 cm (Table 1). Clutch size was 102-120 eggs, but a clutch not taken into consideration for the calculations contained only 2 eggs, or perhaps the turtle aborted the oviposition process, after we accidentally touched its cloaca while trying to remove sand in order to improve our ability to count the number of eggs laid. The nesting female stayed immobilized for another 2 h, after which it covered the nest with elaborate camouflaging and returned to the sea.

The mean size of the nest body chamber was 172.6 cm long (range, 80-260 cm; n = 19 body chambers), 161.31 cm wide (range, 135-220 cm; n = 19), and 42.63 cm deep (range, 35-57 cm; n = 19).

Nesting female turtles generally took 2 h to complete the nesting process, with phases 3 and 7 being the longest (Fig. 3). On the other hand, the duration of exercise-rest cycles showed significant

Table 1. Morphometrics of green turtles *Chelonia mydas* nesting on Ras Al Jinz beaches at the Ras Al Hadd Nature Reserve, Oman. Sampled in 2000 (CI, confidence interval; CCL, curved carapace length; CCW, curved carapace width; PL, plastron length; TL, tail length; W, weight; n, sample size)

Parameter	Mean ± 95% CI	Range	n
Nesting females			
CCL (cm)	102.75 ± 1.87	89.00 - 116.00	36
CCW (cm)	92.86 ± 10.47	83.00 - 110.00	36
PL (cm)	79.28 ± 3.16	75.00 - 87.00	7
TL (cm)	7.57 ± 5.60	5.00 - 9.00	7
W (kg)	116.28 ± 13.11	97.00 - 145.00	7
Hatchlings			
CCL (cm)	3.87 ± 0.05	3.70 - 4.00	17
CCW (cm)	4.02 ± 0.01	4.00 - 4.10	17
Eggs			
Diameter (mm)	39.13 ± 0.50	34.00 - 43.00	5 eggs/clutch; 3 clutches
Clutch size (total eggs)	110.66 ± 10.19	102.00 - 120.00	3 clutches
Fertilized eggs (%)	10.66 ± 3.97	7.00 - 14.00	3 clutches

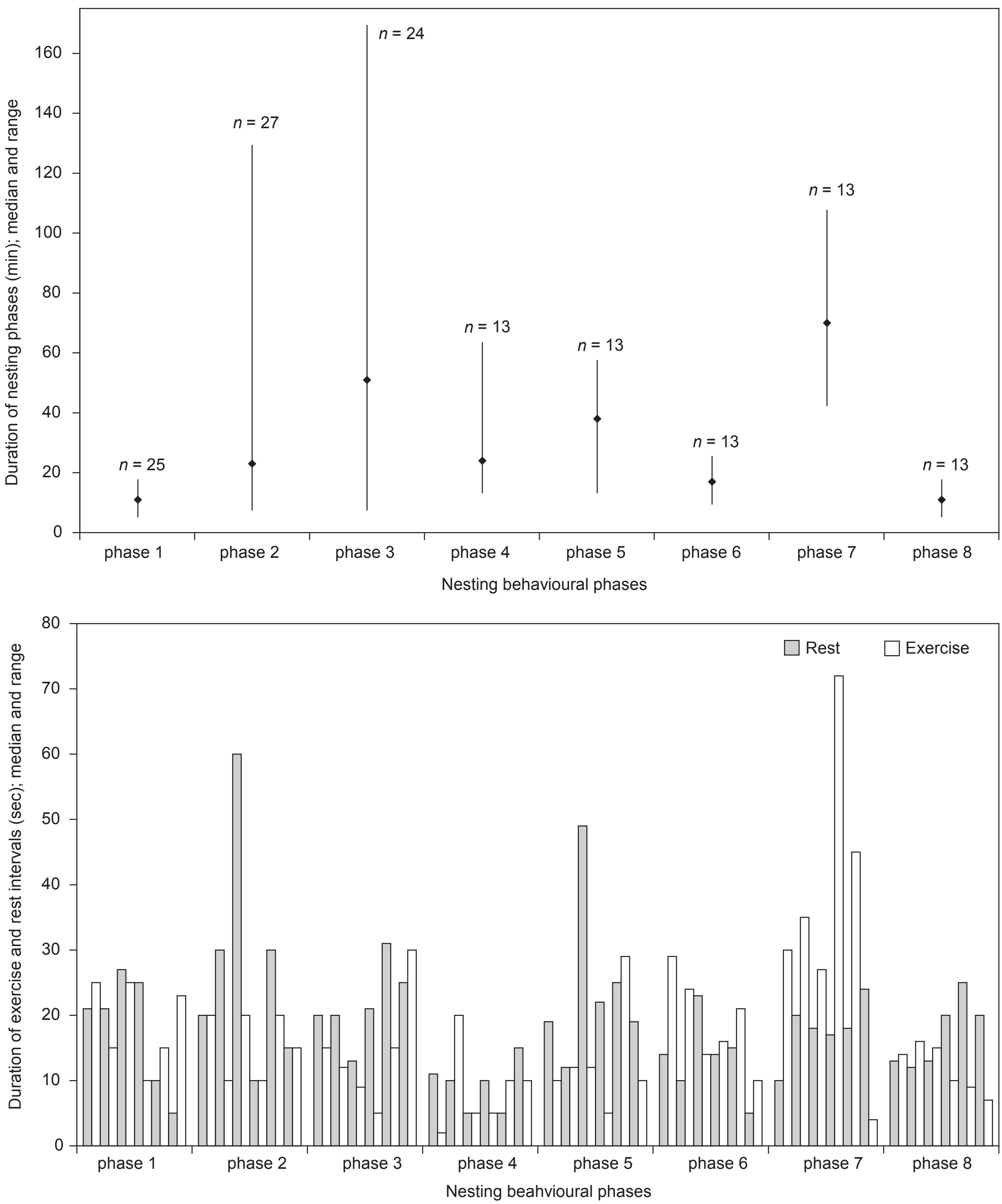

Fig. 3. Top: Nesting behavioral phases of green turtles *Chelonia mydas* at Ras Al Jinz beaches, Ras Al Hadd Nature Reserve, Oman. Bottom: Duration of exercise and rest intervals of 4 nesting sea turtles completing the nesting cycle (*p significant between intervals of rest and exercise intervals, during phases 1 and 8; by ANOVA and Bonferroni's test). Results of both graphs recorded in 2000 in section 2 (size of tested sea turtles: 85 cm < curved carapace length < 95 cm).

differences among the nesting phases, as there were significant differences between the rest and exercise intervals during phases 1 and 8.

Predators of turtle eggs and hatchlings and their diets

The potential predators of sea turtle eggs and hatchlings, identified at Ras Al Jinz beaches, in 1999-2001 and 2009 included ghost crabs, birds, and terrestrial mammal carnivores. There were no differences from year to year, either in species composition or abundance.

Ghost crabs *Ocypode* spp. holes were present at abundances of 0-10 crab holes/m^2 in supralittoral areas. No crab holes were observed on the intertidal, but often groups of up to 50 ind. were standing by the water in the early hours, waiting to catch sea turtle hatchlings. Also some of the crab holes communicated with the egg chamber of sea turtle nests.

The most commonly observed bird species, year round, at Ras Al Jinz beaches were herons (*Ardea cinerea* 2 ind./km/yr and *Egretta gularis* 4 ind./km/yr; although they were frequently observed in larger numbers feeding in the nearby khawrs, 10 ind./km/yr for the 2 species combined), seabirds (gulls *Larus hemprichii*, 300 ind./km/yr and terns *Sterna* spp. 500 ind./km/yr), and house crows *Corvus splendens* (2 ind./km/yr). Only crows were observed nesting at Ras Al Jinz beaches. Birds were not a threat to sea turtle eggs, but if the hatching process took place during daylight hours or even during full-moon nights, seagulls in particularly would try and catch all of the hatchlings trying to reach the sea.

The red fox *V. v. arabica* was identified as the most important sea turtle egg and hatchling predator on the nesting grounds at Ras Al Jinz beaches, Ras Al Hadd Nature Reserve, Oman. Other terrestrial mammals identified as potential predators of turtle eggs and hatchlings at the Ras Al Hadd Nature Reserve included Rüppel's sand fox *V. rueppellii sabaea*, Blandford fox *V. cana*, Arabian wolf *C. lupus arabs*, mongoose *Ichneumia albicauda albicauda*, wild cats *Felis* spp. and *Caracal caracal schmitzi*, and hyenas *Hayena hayena sultana* (Table 2, Fig. 4). Direct observations of fox activities on Ras Al Jinz beaches showed that foxes caused relatively high mortality of eggs and hatchlings. All canids are equipped with a developed olfactory sense and therefore can easily find underground sites of sea turtle nests. At the Ras Al Jinz beaches, foxes usually did not dig for eggs during the night as the relatively high density of sea turtles, nesting on top of previously laid clutches, often left exposed sea turtle eggs, which were collected by foxes and also eaten by wild cats and birds. However, during the early hours of the day, 1-2 ind./km^2 were observed invading turtle nests for eggs.

Foxes were also observed feeding on sea turtle hatchlings at the hunting ground, and causing further mortality by chewing off a small bite of a relatively large number of prey (ranging 10-20 hatchlings per night caught per individual fox), in order to kill the prey for storage for later consumption, or as a hedge against future food shortages. However, as the next day brought a new supply of fresh food, the stored food was rarely eaten, but foxes repeated this strategy, day after day, and killed hatchlings daily, resulting in

Table 2. Recorded abundances (on a logarithmic scale) of terrestrial carnivore mammal species at Ras Al Jinz beaches, Ras Al Hadd Nature Reserve, Oman

English name	Species	Abundance (log. no. of individuals/km^2)
Arabian grey wolf	*Canis lupus arabs*	0-1
Red fox	*Vulpes vulpes arabica*	10-100 (near sea turtle nesting beaches) 1-10 (further inland)
Rüppels' sand fox	*Vulpes rueppellii sabaea*	1-10
Blandford's fox	*Vulpes cana*	1-10
White-tailed mongoose	*Ichneumia albicauda albicauda*	1-10
Striped hyena	*Hyaena hyaena sultana*	0-1
Sand cat	*Felis margarita harrisoni*	1-10
Gordon wild cat	*Felis silvestris gordoni*	1-10
African wild cat	*Felis silvestris lybica*	1-10
Caracal lynx	*Caracal caracal schmitzi*	0-1

large numbers of hatchlings being stored on the ground of areas nearby the sea turtle nesting beaches. Any hatchlings left exposed on the beaches were quickly removed by seabirds and crabs during the early hours of the day.

It was not always possible to identify the fox species moving during the night hours on the sea turtle nesting beaches, unless it was a relatively large individual; therefore, it was unmistakably identified as an adult red fox, the larger species in the area. Also, it was not possible to distinguish which fox species had stored the food at a specific site, although it is more likely that storage places near the intertidal caves were used by red foxes, which displaced the smaller-sized Blandfor's foxes and Rüppell's sand foxes. The smaller-sized foxes occupied caves located further inland. Also there was no difference in hunting strategic behavior on the sea turtle nesting beaches, as every individual fox displayed the same pattern, independent of body size and time of the year. Scat analyses indicated that fox diets were composed primarily of sea turtle eggs and hatchlings (Fig. 5), and showed no significant differences either between the sea turtle higher-density and lower-density nesting season or between sites ($p > 0.05$; by two-way ANOVA and the Bonferroni test).

Impacts of the fox community

As nesting female turtles came to nest from just after sunset up to about 02:00 (rarely coming later), they did not interact with birds. However, sea turtles coming to nest during dark hours at the Ras Al Jinz beaches were able to recognize and avoid terrestrial carnivores and humans, as observed from the 3 experiments.

Results from experiment 1 showed that sea

Fig. 4. Some terrestrial carnivore mammals on sea turtle nesting grounds in Oman: Arabian grey wolf *Canis lupus arabs* (A), Arabian red fox *Vulpes vulpes arabica* (B), hyena *Hayena hayena sultana* (C), Rüppel's sand fox *V. rueppellii sabaea* (D), Gordon's wild cat *Felis silvestris gordoni* (E), and caracal *Caracal caracal schmitzi* (F). (Photos: Ministry of Environment, Oman).

turtles nested in significantly higher numbers on the undisturbed section of the beach than on disturbed sections (Fig. 6), with total numbers of nests of 125 (equivalent to 0.04 nests/m^2), 253 (equivalent to 0.08 nests/m^2), and 138 (equivalent to 0.04 nests/m^2), respectively, for sections 1 (disturbed by fishermen), 2 (undisturbed), and 3 (disturbed by natural predators). Undisturbed areas also differed from the others in terms of nest placement, as in undisturbed areas, nests were more abundant 15-45 m from the surf's edge, contrary to what was observed in sections 1 and 3, where nests were more abundant closer to the surf's edge. There were no significant differences among the 5 sampled days ($p > 0.05$; by ANOVA and the Bonferroni test).

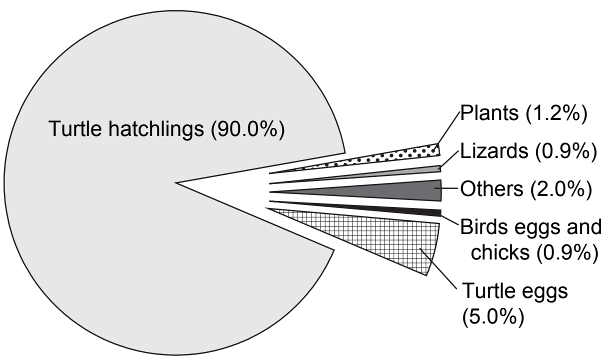

Fig. 5. Diets (overall relative frequency of prey representation in volume) of Arabian red foxes *Vulpes vulpes arabica* at Ras Al Jinz beaches, Ras Al Hadd Turtle Reserve, Oman. ('others' included marine gastropods, ghost crabs, insects, and fish).

Experiment 2 demonstrated that turtles significantly increased their efforts to camouflage their nests if they sensed the presence of foxes or people after they already had begun oviposition (Fig. 7).

Finally, experiment 3 showed that at Ras Al Jinz beaches, only 1/2 of the nesting sea turtles that ascended the beach to nest completed the nesting process (Fig. 8). In fact, all female turtles disturbed before beginning oviposition, either by foxes, humans, or other turtles, returned to the sea without trying again. All turtles that abandoned the 1st nesting site due to sand collapsing tried another nesting site before returning to the sea. During both the higher- and lower-density nesting season, the main causes for nest site abandonment were disturbance by foxes or humans, and sand characteristics. Intraspecific competition for nesting site was also a cause for nest site abandonment, especially during the lower-density nesting season. Interestingly, in Oct. 2000, a green turtle finally laid eggs after abandoning 12 previous sites, where the body pit was excavated; it took her a total of 5 h and 8 min to return to the sea after ascending to the beach to lay her eggs.

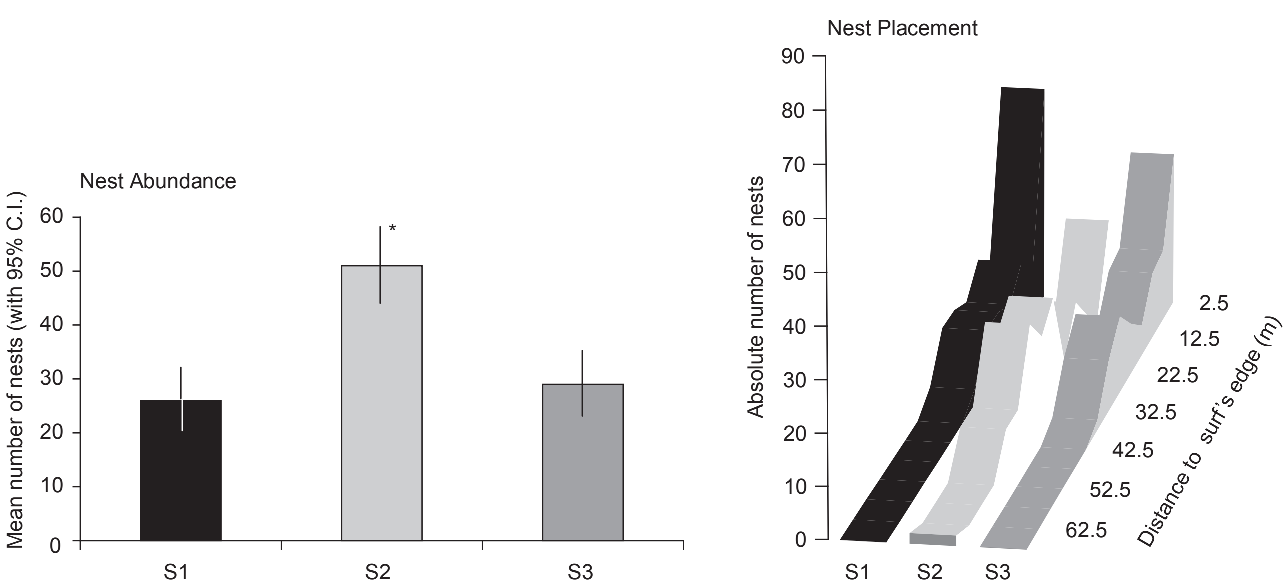

Fig. 6. Mean number of nests (**p* significant, by ANOVA and Bonferroni's test; n = 10 d, differences non-significant between days in the same season; C.I. are confidence intervals) and nest placement (n = 10 d; differences non-significant between days in the same season, by ANOVA; size of tested sea turtles: 85 cm < curved carapace length < 95 cm) on each section (S1: high concentration of fishermen, S2: relative absence of both fishermen and foxes, and S3: high concentration of foxes).

DISCUSSION

Nesting sea turtles at Ras Al Jinz

Although this study only examined the behavior of green turtles *C. mydas*, it may be applicable to other turtle species, as according to Hendrickson (1995), sea turtles show remarkably little variation between species with respect to the major aspects of their nesting behavior, probably due to their common evolutionary history.

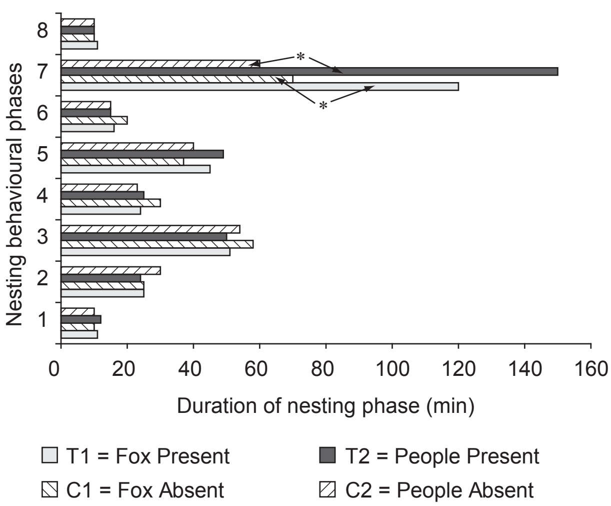

Fig. 7. Nesting behavior in the presence and absence of foxes (treatment 1, T1, and control 1, C1) and humans (treatment 2, T2, and control 2, C2) (*p significant, by ANOVA and Bonferroni's test; n = 10 nesting females per treatment and per control; size of tested sea turtles: 85 cm < curved carapace length < 95 cm).

They have also adopted a short burst of exercise followed by a brief resting pause, resulting in a behavioral pattern which may be of survival value, not only from the point of view of its physiological importance, but also because during the resting phase, nesting females can probably better detect predators and evaluate the conditions of the sediment. In vertebrates, which adopt patterns of short exercise durations, rest cycles trigger respiratory and cardiovascular changes as well as neuroendocrine activation and a metabolic shift associated with stress (e.g., West et al. 1992). These processes were studied in fish (e.g., Jensen 1987, Hughes et al. 1988, van Raaj et al. 1996), birds (Le Maho et al. 1992), and turtles (e.g., Wasser and Jackson 1991, Comeau and Hicks 1994, Johnson et al. 1998). Periods of ventilation, which consist of 1 or more breaths, are separated by non-ventilatory periods, and during the rest periods, sea turtles may be particularly alert to the presence of predators. For example, during the later phases of digging, the exercise intervals shortened while the rest intervals lengthened. This condition is typical of intermittent breathers (e.g., Butler et al. 1984). During exercise, the turtles are shallow breathers, but as soon as they pause for

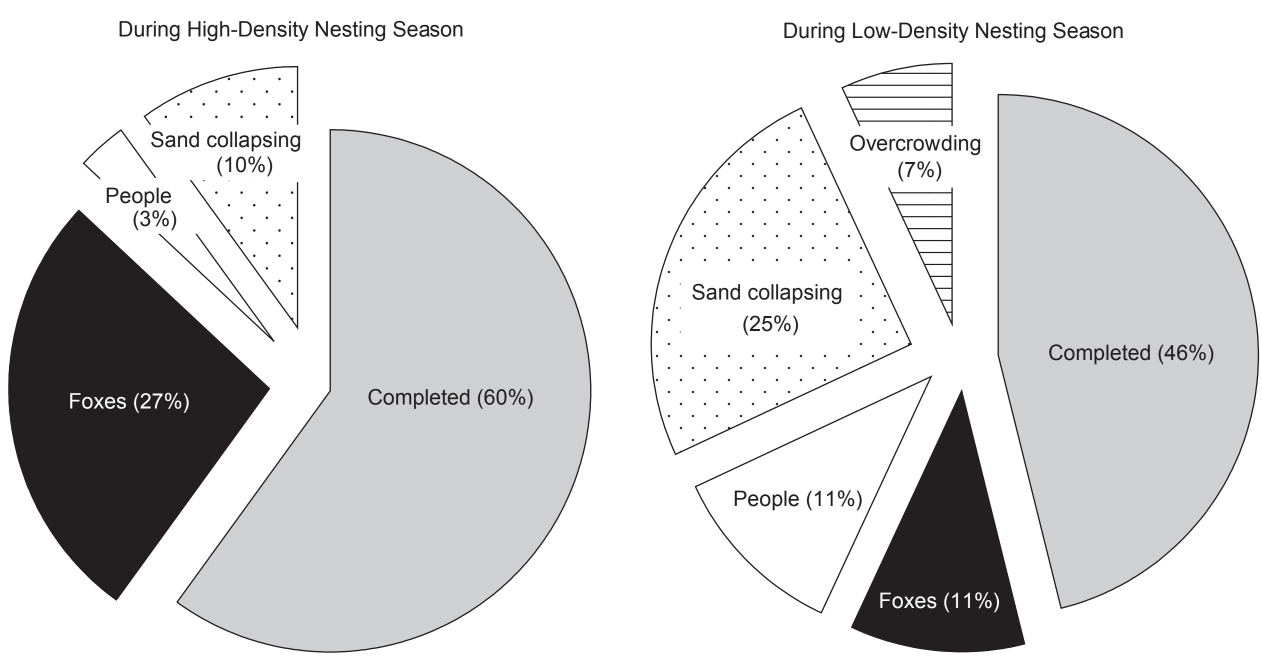

Fig. 8. Reasons for nest site abandonment by female turtles, before they began laying their eggs (n = 32 individuals/season; size of tested sea turtles: 85 cm < curved carapace length < 95 cm).

rest, they inhale a large amount of air with force, to overcome the hypoxic conditions that develop during exercise. Apparently, during exercise, green turtles practice anaerobic metabolism, which leads to acidemia and hypoxia, but they are able to increase their breathing rate in response to hypoxia (Wasser and Jackson 1991, West et al. 1992). The high level of metabolic acidosis associated with exhaustive exercise was also shown to be related to sharp rises in epinephrine and norepinephrine plasma levels in turtles (Wasser and Jackson 1991). These hormones may facilitate removal of lactic acid from muscles to the bloodstream and may also induce oxygen uptake during the rest period.

Predators of turtle eggs and hatchlings and their diets

Although foxes *Vulpes* spp. are known to occur in the area, confirmation of the Arabian wolf *C. lupus arabs* at Ras Al Jinz beaches (both in 1999-2001 and 2009) is an important finding of the present study, as it has not previously been confirmed in the area by the Canid Specialist Group of the International Union for Conservation of Nature and Natural Resources, IUCN (Sillero-Zubiri et al. 2004), despite being listed by Fisher (1999) as a species occurring in Oman.

Results from the scat analyses showed that most of the canids at the Ras Al Hadd Nature Reserve were individuals of the red fox *V. v. arabica*, as other fox species (*V. rueppellii sabaea* and *V. cana*) would have higher proportion of plant materials in their droppings (Table 3). In the Ras Al Jinz area of the Ras Al Hadd Nature Reserve, the intertidal and supralittoral caves provide habitat for this peculiar fox community, which depends almost entirely upon the marine food web (feeding mainly on sea turtle eggs and hatchlings, but also on crabs and gastropods), contrary to other canid populations elsewhere in the region (e.g., Stuart and Stuart 2003, Murdoch et al. 2007) or beyond (e.g., Girard 1998, Muñoz-Garcia and Williams 2005), which are known to feed on small rodents, lizards, birds, and insects. Other red foxes in this specific area, that occupy caves further inland at Ras Al Jinz, away from the sea turtle nesting beaches, beyond the surveyed area, may be less dependent on the marine food web. In fact, Home (2005), based on scat analyses found that the Indian fox *V. bengalensis* in the Gujarat region of India is an opportunistic carnivore species that feeds on invertebrates (beetles, orthopterans, scorpions, and termites), vertebrates (birds, lizards, rodents, hares, sheep, goat, and cattle), and fruits of *Ziziphus* sp. and *Prosopis* sp. Previously, Olfermann (1996) observed diets of Rüppell's foxes in Saudi Arabia and concluded it consisted mostly of arthropods (55%) and rodents (35%), although they also ingested some plants (5%). Recently, Murdoch et al. (2007) studying diets of Rüppell's foxes in the United Arab Emirates recorded the following prey: invertebrates (beetles Tenebrionidae: *Mesostena puncticollis*, *Erodius octocostatus*, and *E. reichei*; and scarab beetles

Table 3. Known parameters for body mass, source of water (diet), and home range of fox species, which are also present at Ras Al Jinz beaches, Ras Al Hadd Nature Reserve, Oman

	Vulpes vulpes	*Vulpes rueppellii*	*Vulpes cana*
Body mass			
	4725 g Williams et al. 2004	1545 g Williams et al. 2004 Murdoch et al. 2007	1285 g Williams et al. 2004
Source of water (diet)			
Vertebrates	98.4%	78.5%	11.7%
Invertebrates	0.1%	7.4%	43.8%
Plants (leaves, fruits, and seeds)	1.5%	13.3%	44.5%
	Kauhala et al. 1998	Lindsay and MacDonald 1986	Geffen et al. 1992
Home range			
	4.12 km^2 Trewhella et al. 1988	13.1 km^2 Lenain et al. 2004	1.08 km^2 Geffen and MacDonald 1993

Scarabaeidae: *Scarabaeus cristatus*) and reptiles (white-spotted lizard *Acanthodactylus shmdtii*, and the sand skink *Scincus mitranus*).

Obviously, for the fox community at the Ras Al Hadd Nature Reserve, it is more profitable from an energetic point of view to hunt turtle hatchlings and dig turtle eggs (or even to eat eggs accidentally exposed by turtles nesting on top of previous nests) rather than spending energy chasing rodents and lizards, which are scarce in the desert. In fact, Williams et al. (2002) found metabolic adaptations of Rüppell's foxes in the desert of the Arabian Peninsula, by testing the hypothesis that foxes have a reduced basal metabolic rate (BMR) and total evaporative water loss (TEWL) when in captivity and a reduced field metabolic rate (FMR) and water loss when in the wild. In captivity, males (averaging 1858 g in body mass) had an oxygen consumption of 914.9 mL O_2/h (equivalent to 441.4 kJ/d), whereas females (averaging 1233 g) consumed 682.9 mL O_2/h (equivalent to 329.4 kJ/d). The mean TEWL was 52.6 g H_2O/d for males and 47.5 g H_2O/d for females. In the wild, during winter, males expended energy at a rate of 1306.5 kJ/d and females at a rate of 722.8 kJ/d. Water flux in the wild showed no significant differences between sexes and averaged 123 mL H_2O/d, a value 30% lower that that observed in foxes in the deserts of southern North America (Girard 1998). Finally, no evidence of a reduced BMR compared to other carnivores or other foxes elsewhere was found, but from their TEWL measurements in a controlled environment (in captivity), there was an indication of evolutionary specialization in their respiration and cutaneous water loss. Also Muñoz-Garcia et al. (2005) concluded that the BMR of the Carnivora was positively correlated with home range size after controlling for body mass (Table 3). In addition, diet and the mass-adjusted home range size were correlated. When testing the effects of diet and mass-adjusted home range on the mass-adjusted BMR, home range size was insignificant because of its colinearity with diet. Furthermore, Gastron (2009) explained how the geographic range of a species is shaped by dispersal limitations, physiological limitations, and species interactions.

Impacts of the fox community

In the present study, sea turtles behaved similarly in the presence of people/human activities and natural predators, probably because both are general forms of disturbance, but similar studies on interactions with terrestrial mammals on turtle nesting grounds elsewhere are still not available for comparison. In the present study, there was a relationship between disturbance and nest placement, although other factors such as characteristics of the sediment and intraspecific competition for space were not tested, and they could have played a role (e.g., Chen and Cheng 1995). Disturbed turtles nested closer to the tidal mark, probably avoiding leaving their clutches too far from the water, which would increase the distance that hatchlings would need to travel on the beach; therefore, reducing their exposure to predators. Both natural predators and human presence obviously stressed these sea turtles, affecting their decisions on nest site selection, and this may have had indirect consequences for hatchling survival and even the sex ratio (e.g., Wang and Cheng 1999), as sex in turtles is determined by the incubation temperature (e.g., Stoneburner and Richardson 1981, Martin 1988), and even a change of 1-2°C can make a considerable difference to the sex ratio of hatchlings (e.g., Janzen and Paukstis 1991, Mrosovsky and Yntema 1995). Therefore, nest-site selection by nesting sea turtles should be related to the sand temperature gradient (Stoneburner and Richardson 1981), but Bjorndal and Bolten (1992) were unable to demonstrate any clear selection pattern among green turtles at Torturego, Costa Rica. On the other hand, many studies showed that nest-site selection may be related to several characteristics of the beaches (such as topography, including slope, microhabitats, submerged rocks, and vegetation; e.g., Mortimer 1990 1995), light pollution, and even human disturbance (e.g., Witherington and Martin 1996). As suggested but not tested by other authors (e.g., Mortimer 1995), biotic factors such as predation on eggs and hatchlings, and intraspecific competition among nesting females (for nest sites) may be more important than purely physical and geological characteristics of the beaches. In fact, predation pressure on turtle eggs and hatchlings may be the most important factor affecting nest-site selection by nesting females.

As also observed by Johnson et al. (1995 1996), sea turtles at Ras Al Jinz increased their efforts to camouflage their nests when they spotted people on the beach. However, as observed by Jessop et al. (2000), stress may also induce enhanced reproduction rates in sea turtles as a response to adverse conditions. When nesting turtle densities were reduced from Oct., nesting females seemed more relaxed as far as intraspecific competition for nesting sites was concerned, and this was probably reflected in their apparently increased fussiness in choosing a nest site and in their awareness of predators.

From the experiments conducted in the present study, a common pattern of behavior was clear: female turtles avoided predators (foxes) and people. Therefore, the presence of humans and or signs of human activities (e.g., boats, nets, and lights) should be restricted to selected beaches, away from beaches as important as Ras Al Jinz. Additionally, guided visits should be especially strict regarding unsuitable behavior of tourists, especially during the lower-density nesting season when sea turtles are particularly aware of disturbances.

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