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Ecology of lowland lizards in the eastern United Arab Emirates

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(With 3 figures in the text)

Aspects of the ecology of 23 lizard species found in the coastal lowlands of eastern Arabia are reported. The majority of these forms occur in arid environments and the most obvious ecological separation is between diurnal and nocturnal species, the ten latter forms all being geckos. Within these two groupings, species differ principally in microhabitat (particularly such features as distance from vegetation and ground softness), hunting techniques ("sit and wait", active search or slow visual scanning) and the size of their mainly arthropod prey. However, two large diurnal forms are food specialists, feeding largely on plants and small vertebrates, respectively, and some diurnal species show differences in their time of activity during the morning. Body temperature of day-active species, which are all essentially heliothermic, is controlled by posture, retreat into shade or burrows and the use of the ground as a heat sink. Usual activity temperatures show correlation with normal time of activity during the morning and the amount of shade cover available. Substantial interspecific variation exists in the extent to which body temperature is regulated. Most nocturnal forms have body temperatures close to the ambient but they may sometimes be elevated in *Bunopus tuberculatus,* perhaps as a result of utilizing underground warmth. A wide range of predator avoidance techniques are used, including fleeing, hiding in burrows, burial in loose sand and caudal autotomy. The proportion of damaged tails is higher in climbing species than in ground-dwelling ones. Females are mainly gravid in the spring. The number of eggs carried is low in species of small body size (often one or two), suggesting that egg-laying is repetitive. Contrary to accepted opinion, clutch size is variable in some gekkonine species, either one or two eggs being laid. Hatchlings appear largely in the late spring and summer. A number of morphological features correlate with niche characteristics: gross body shape is related to hunting and escape technique, foot structure to substratum type, and species living on soft sand have modifications that exclude sand from the body orifices. The lizard fauna discussed here extends with only restricted change over much of Arabia. The faunas of the extreme south west of the peninsula and of the Sahara are generally similar to it, but differ substantially in the species they contain, and possibly in the pattern of occupied niches as well.

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Introduction

In the last two decades, much work has been carried out on the comparative ecology of desert lizards, especially by Pianka and his associates, and the eremean faunas of North America, Australia and South Africa have all been surveyed (see Pianka, 1977, for a selection of references). In contrast, relatively little has been published about the ecology of the lizards of the great Saharo-Arabian desert, although scattered information exists, for instance in the papers of Mosauer (1932, 1934) and Gauthier (1967) dealing with the north-western Sahara, and those of Duvdevani & Borut (1974), Frankenberg (1974, 1978), Werner (1965, 1968, 1969), Werner & Broza (1969) and Werner & Goldblatt (1978) discussing aspects of species found in Palestine. For Arabia, some observations have been reported from the more mesic, peripheral areas, such as the mountains of northern Oman (Arnold & Gallagher, 1977) and Dhofar, southern Oman (Arnold, 1980*a*), but none from really desertic regions. The present paper deals with a predominantly desert lizard community from eastern Arabia, many of the forms discussed being widespread in the peninsula.

Area covered

The region studied lies on the southeast coast of the Arabian Gulf in the eastern United Arab Emirates. It extends from Ash Sha'am (26·02N, 56·05E) southwest to Ras Ghanada (24·50N, 54·45E) and to the east is bordered by the North Oman mountains (the Western Hajar). Substantial areas are covered by sand dunes which vary in height from a few centimetres to more than 50 m. Those on the coast are made up of carbonate sands formed of broken shells, while further inland they have been produced from weathered quartz rocks. In many places, the dunes are at least partly stabilized by vegetation but in others, especially in the south, they are active with mobile slip faces. Dunes are interspersed with flat alluvial areas that are more developed and largely continuous along the edge of the mountains. These have surfaces ranging from very fine sediment to gravel and, in general, are considerably harder than those encountered in dune areas. Mainly near the coast, there are salt flats or sabkhas consisting of embayments of the sea full of evaporites, especially gypsum (Kendall & Skipwith, 1969). They may have a crusted surface, or be moist and sticky, and usually lack vegetation, except at their edges where there are often extensive stands of low halophytes such as *Zygophyllum qatarensis* Hadidi, *Halopeplis perfoliata* (Forssk.) Bunge ex Aschers & Schweinf. and *Halocnemum strobilaceum* (Pall.) Bieb.

The three main ground types are often complexly interspersed where they contact each other, so that extensive ecotonal areas exist. Near the coast and along the mountain plain, there are isolated areas of lush vegetation in the form of plantations and gardens, virtually all of which are dependent on artificial irrigation. The environment of the region is more fully discussed by Satchell (1978).

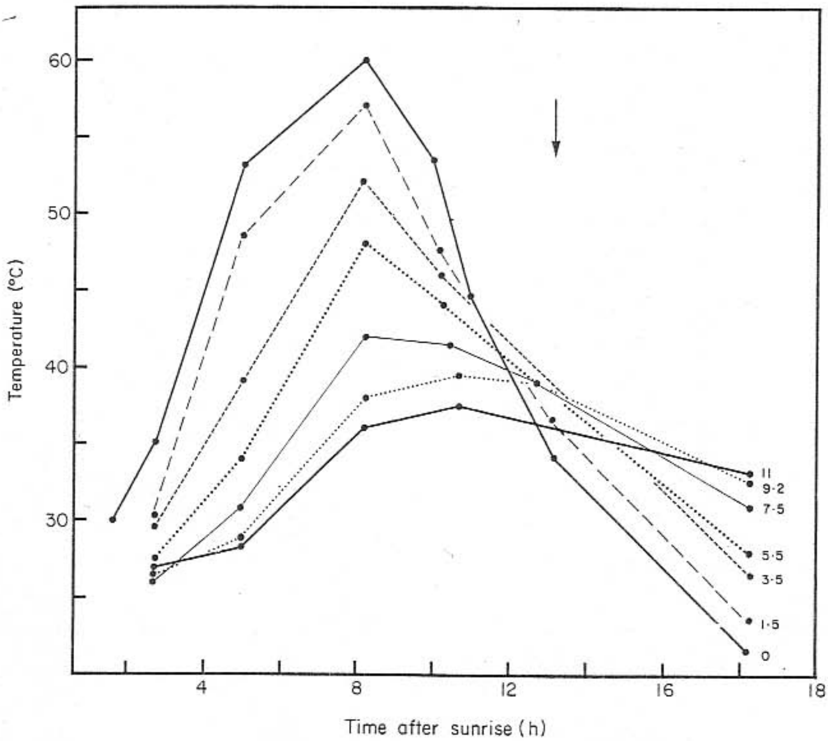

FIG. 1. Change in temperature of level sand exposed to the sun at Sharjah on 30 April 1973. Lines represent different depths below surface and associated figures indicate these in cm. The arrow shows time of sunset.

Climate and ground temperatures

The climate is severe, with temperature extremes of about 49°C in July and 4°C in January, the hottest months being June to September. Humidity in summer is very high, but rain falls mainly as showers between November and April, mean annual precipitation being about 100 mm. Insolation is intense with ground temperatures sometimes exceeding 65°C during the day in summer. Ground temperatures show a very marked diel cycle. This is strongest at the surface, but can be detected at depths of some centimetres. Not only do lower levels show less change, but they reach their maximum temperatures later in the day than the surface layers and cool more slowly (Fig. 1). This means that there is a marked reversal in vertical temperature gradient. The surface becomes increasingly hotter than the lower levels until about the middle of the day, but by sunset it is cooler than them, and this reversal lasts for some hours. Such temperature differences are important in the thermoregulation of many lizards. As the surface warms up, some diurnal species dig so that they can place their bodies in contact with the cooler layers beneath and use them as a heat sink to reduce net heat uptake. Conversely, stored ground heat keeps the surface temperature relatively high in the evenings, in spite of loss by radiation into the usually very clear atmosphere, enabling nocturnal species to maintain adequate temperatures for activity for longer than would otherwise be the case. At least one night-active gecko may use sub-surface heat directly to raise its temperature (p. 347).

Methods of investigation

The area was visited on 2 occasions: 21 March–5 April, 1971 and 18 April–24 June, 1973. A variety of study methods was used.

(1) A range of habitats were walked over and as many of the following features as possible noted for each individual lizard seen: (a) species, (b) sex and maturity (adult, part-grown or juvenile), (c) time of initial sighting, (d) kind of substratum (e.g. sand, alluvium or sabkha), either (e) height above ground for climbing species, or (f) ground softness for terrestrial ones, (g) distance from nearest vegetation, (h) distance fled to a refuge, (i) kind of refuge used.

Ground softness was assessed by dropping a narrow, smooth rectangular steel plate end on from a height of 0·5 m and noting the extent of its penetration in 10 mm units. The plate was 300 mm long, 28·5 mm wide and 1 mm thick and weighed 70 g. Although this method usually gave a reasonable indication of surface ground softness, it could sometimes be misleading, for instance if a thin layer of soft loose sand overlaid harder material. Distance from nearest vegetation was assessed excluding plants too small to give significant cover, i.e. those less than 50 mm high and 100 mm across.

Habitats were examined at as many times of day as possible and also at night. In spring, diurnal lizards are largely active in the morning with sightings becoming sparse around mid-day, but for many forms there is another more minor period of activity in the late afternoon.

(2) Some lizards were noosed, or shot using a 0·22 pistol loaded with dust shot, and their body temperatures taken using a Schultheiss mercury thermometer inserted into the cloaca.

(3) Individual lizards were watched, with binoculars where necessary, for extended periods, so that some idea of hunting strategies could be gained. In soft-sand areas, additional information on foraging techniques was sometimes obtained from following tracks of foot-prints.

(4) Animals preserved for taxonomic investigations and deposited in the British Museum (Natural History), London were also used in some cases, to check diet, season of egg production, clutch size and incidence of tail autotomy.

Where appropriate, so-called niche overlap and niche breadth (Pianka, 1973) were calculated for the various ecological parameters observed for each species.

Niche breadth is quantified as;

$$B = \frac{1\Big/\sum_{i}^{n} P_i^2}{n},$$

where P_i is the proportion of the ith resource used where the niche dimension (e.g. ground softness, time of activity) is divided into n categories.

Niche overlap between two species is quantified as:

$$O_{jk} = O_{kj} = \frac{\sum_{i}^{n} P_{ij} P_{ik}}{\sqrt{\sum_{i}^{n} P_{ij}^2 \sum_{i}^{n} P_{ik}^2}},$$

where P_{ij} and P_{ik} are the proportions of the ith resourse used by the jth and kth species.

Major niche differences

It is apparent from the observations described above that the niches of lowland lizards in the eastern United Arab Emirates are differentiated by the same main parameters that separate lizards ecologically elsewhere: time, space, diet and hunting methods. The species present fall into two clear groups as regards time: those that forage by day and those by night. The former also show some staggering of activity among themselves. Spatial separation involves a distinction between habitual climbers and non-climbers and, among the latter, a division by substratum type. In addition, some species are associated with arid areas and others with relatively humid ones. With the exception of a couple of food specialists, it seems likely that prey size is more important than prey type in separating species ecologically. Finally, there are substantial differences in hunting strategy. Most species are mainly "sit and wait" foragers or active searchers (MacArthur & Pianka, 1966; Schoener, 1971; Pianka, 1973), but a few geckos use a different technique described here as slow visual scanning.

Large, mainly diurnal species

Two species are much larger than the others and also differ in not feeding principally on arthropods when adult, although they take them when young. These are the agamid, *Uromastyx microlepis,* and the monitor, *Varanus griseus.* The former is usually encountered on relatively hard alluvial surfaces, where it occurs in colonies living in burrows. Faeces and stomach contents confirm that mature animals are overwhelmingly vegetarian. Mandeville (1965) describes the composition of the diet. *Varanus griseus* is also ground dwelling, but is regularly found on a wider variety of ground types, ranging from coarse gravel to aeolian sand. The few stomach contents available from Arabian specimens indicate that it feeds on a variety of vertebrates, including small mammals and lizards (*Acanthodactylus, Scincus* and even *Uromastyx*). *Varanus griseus* is an active hunter. Tracks followed for over 500 m across soft sand clearly show that it digs for prey at rodent burrows and those of *Acanthodactylus schmidti.*

Diurnal lizards found on soft sand

Three species belonging to different families are regularly associated with soft sand habitats. These are the skink, *Scincus mitranus,* the lacertid, *Acanthodactylus schmidti,* and the agamid, *Phrynocephalus arabicus.* They differ markedly in most of the ecological parameters examined (see Tables I–IV).

Differences in microhabitat

Acanthodactylus schmidti and *P. arabicus* are usually found on relatively firm sand, whereas *S. mitranus* is typically encountered on much softer surfaces, nearly always the slip faces of mobile dunes and areas bordering them. While *A. schmidti* is usually seen close to bushes or other fairly low vegetation, the other two species often occur at some distance from such cover. Thus, although *A. schmidti* and *P. arabicus* both live on relatively firm sand, the former is largely confined to areas where the sand is partly stabilized by root systems, while the latter is found in flattish, open areas of often rippled sand which is firm, mainly because the grains are closely packed together. These two parameters, ground softness and distance from vegetation, separate most members of each species from the others (Fig. 2).

TABLE I

Variation in some ecological parameters of small diurnal lizards. Entries are percentages of lizards observed

	Ground softness													
Softness units (see p. 332)	0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18–20		*n*	Mean	Niche breadth
Scincus mitranus			4·5	9·0	6·0	18	29·9	24·0	6·0	3·0		67	12·61	0·378
Acanthodactylus schmidti	1·2	7·3	35·3	51·2	3·6		1·2					82	6·07	0·250
Phrynocephalus arabicus		6·9	48·6	40·2	2·8	1·4						72	6·0	0·200
Mesalina adramitana	63·6	23·6	12·7									55	1·48	0·208
Mesalina brevirostris	50·0	44·1	5·9									34	2·15	0·191
	Distance from vegetation when first seen (m)													
	0–2	2–4	4–6	6–8	8–10	10–12	12–14	14–16	16–18	18+				
Scincus mitranus	20·9	9·7	21·0	6·5	8·6	6·5	9·7	11·3	1·6	11·3		62	6·21	0·581
Acanthodactylus schmidti	89·6	10·4										58	0·97	0·083
Phrynocephalus arabicus	27·3	31·8	13·6	13·6	4·5	3·0	3·0			3·0		66	4·67	0·430
Mesalina adramitana	91·9	5·4										37	0·89	0·079
Mesalina brevirostris	45·5	48·5	6·0									33	1·16	0·107
	Time after sunrise (h)													
	1–2	2–3	3–4	4–5	5–6	6–7								
Scincus mitranus	50·0	48·5	1·5									66	2·03	0·297
Acanthodactylus schmidti	6·2	39·5	40·7	13·6								81	3·06	0·468
Phrynocephalus arabicus	1·2	15·5	41·7	23·8	16·7	1·2						84	3·97	0·528
Mesalina adramitana	4·9	24·2	37·7	23·0	9·8							61	3·53	0·355
Mesalina brevirostris	5·8	47·0	38·2	5·8	2·9							34	3·12	0·279
	Distance run to first refuge (m)													
	0·5	0·5–1	1–2	2–4	4–6	6–8	8–10	10–12	12–14	14–20	20+			
Scincus mitranus	82·4	4·1	4·1	6·8		1·4		1·4				74	0·71	
Acanthodactylus schmidti	31·0	14·3	26·2	11·9	7·1	9·5						42	2·45	
Phrynocephalus arabicus	2·4	2·4	7·1	14·3	9·5	11·9	9·5	2·4	7·1	19·0	14·3	42	6·5	
Mesalina adramitana	26·4	20·8	13·2	24·5	9·4	3·8						53	2·41	
Mesalina brevirostris	10·0	21·2	21·2	33·3	12·1	3·0						33	2·53	

Times of activity

Scincus mitranus appears early in the day and is the first species to retreat after the morning period of activity (last sightings less than 3·5 h after sunrise). The activity period of *A. schmidti* is rather later (last sightings 4·5 h after sunrise) and that of *P. arabicus* later still (some animals active 6·5 h after sunrise). This staggering of the period when most foraging takes place limits possible interaction between *S. mitranus* and *P. arabicus* considerably, reinforcing the almost complete separation between the two species based on ground softness.

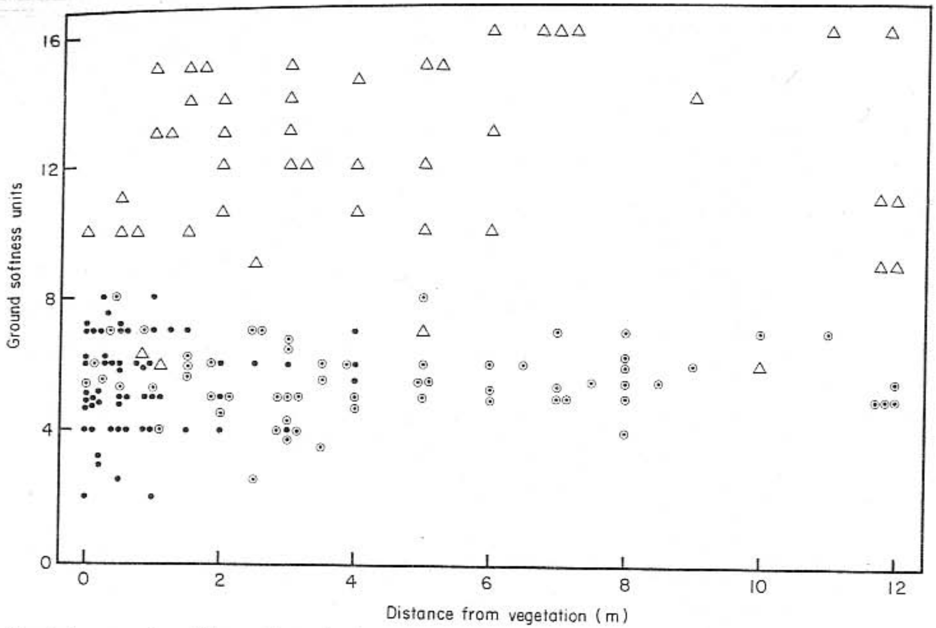

FIG. 2. Spatial separation of three diurnal soft-sand species based on ground softness and distance from vegetation when first seen. △ *Scincus mitranus;* ● *Acanthodactylus schmidti;* ⊙ *Phrynocephalus arabicus.*

Hunting techniques

Scincus mitranus hunt actively on and around slip faces. They often walk jerkily and slowly over the sand, touching it with their tongues and probing the surface layers with their snouts. At times, they dive into the sand with a sinuous motion, so that half the body is buried, and sometimes surface with food. Probably, the initial probing with the snout, and occasionally the whole head, allows prey to be located by scent or sound. These skinks also investigate bush bases and vegetation half buried in the sand, and will chase wind-blown objects across slip faces. The area covered by a single animal in a morning's hunting often exceeds 40 m of a slip face, which may be crossed and re-crossed, and from which the lizard makes excursions on to firmer sand. This may be to hunt, but skinks also move onto firmer surfaces when travelling to a more distant part of the slip face, probably because running is much easier here than on the soft, angled slip itself.

Acanthodactylus schmidti is also an active hunter and adopts a similar technique, walking jerkily over the sand, touching the ground regularly with its snout and probably scenting with its tongue. The snout is often pushed into the sand, rather like a wading bird sticks its bill into mud, and prey may be caught, but the head and foreparts are never submerged in the same way as in *S. mitranus.* Also as in this species, plants and leaf litter are investigated and flying or wind-blown objects may be chased.

Unlike the other species, *P. arabicus* is essentially a "sit and wait" hunter. Individuals stop still in full sun in open places, usually standing high on their legs with the head raised. They often remain like this for 10 or 15 minutes at a time, turning their heads to watch objects as they fly or are blown past, and occasionally dashing forwards to snap up an insect. A particular foraging position is often abandoned suddenly and the lizard runs to take up

TABLE II
Prey size of diurnal lizards living on soft sand (based on stomach contents of 25 adults of each species)

Prey type	Prey size (mm) 0–10	10–20	20+	*n*
Number of prey items (%)				
Scincus mitranus	65	26	9	86
Acanthodactylus schmidti	84	14		320
Phrynocephalus arabicus	94	6		155
Volume of prey (%)				
Scincus mitranus	8	60	32	
Acanthodactylus schmidti	83	17		
Phrynocephalus arabicus	84	16		

a new one, sometimes covering 20 m or more before it stops. Stomachs examined contain some cryptic prey, insect larvae of various sorts that are unlikely to be caught by "sit and wait" hunting, so *P. arabicus* may also forage actively at times, as its congener, *P. helioscopus*, does in Central Asia (Terent'ev & Chernov, 1949). Captured prey is masticated very rapidly once taken, but large insects are often ignored, even if they settle nearby.

Diet

Stomach contents of 25 adults of each species were examined. Although too much reliance should not be placed on such small samples, a number of dietary differences appear to exist. As might be expected from its larger head and body size, *S. mitranus* takes a much higher proportion of big prey than the other species, both judged by number and by volume of prey in each size class (Table II). Diet in all three species is largely or entirely made up of a wide variety of arthropods, but *S. mitranus* also take significant amounts of plant material (leaves, seeds, etc.) that are unlikely to have been ingested accidentally and, in one instance, had eaten a small *Phrynocephalus arabicus*.

Volume of prey

S. mitranus—Coleoptera 43%, insect larvae 22%, arachnids 14%, plant fragments 11%. *A. schmidti*—Coleoptera 28%, ants 22%, Diptera and other flying insects 13%, insect larvae 11%. *P. arabicus*—Diptera and other flying insects 22%, Orthoptera 17%, Isoptera 17%, arachnids 15%.

Number of prey items

S. mitranus—insect larvae and pupae 30%, Coleoptera 28%, plant fragments 20%. *A. schmidti*—ants 46%, Isoptera 31%, Coleoptera 12%. *P. arabicus*—Isoptera 34%, ants 30%, Hemiptera 11%.

Stomachs containing prey

S. mitranus—Coleoptera 48%, insect larvae 32%, plant remains 44%. *A. schmidti*—ants 60%, Coleoptera 48%, insect larvae 28%. *P. arabicus*—ants 28%, Orthoptera 28%, Diptera and other flying insects 24%.

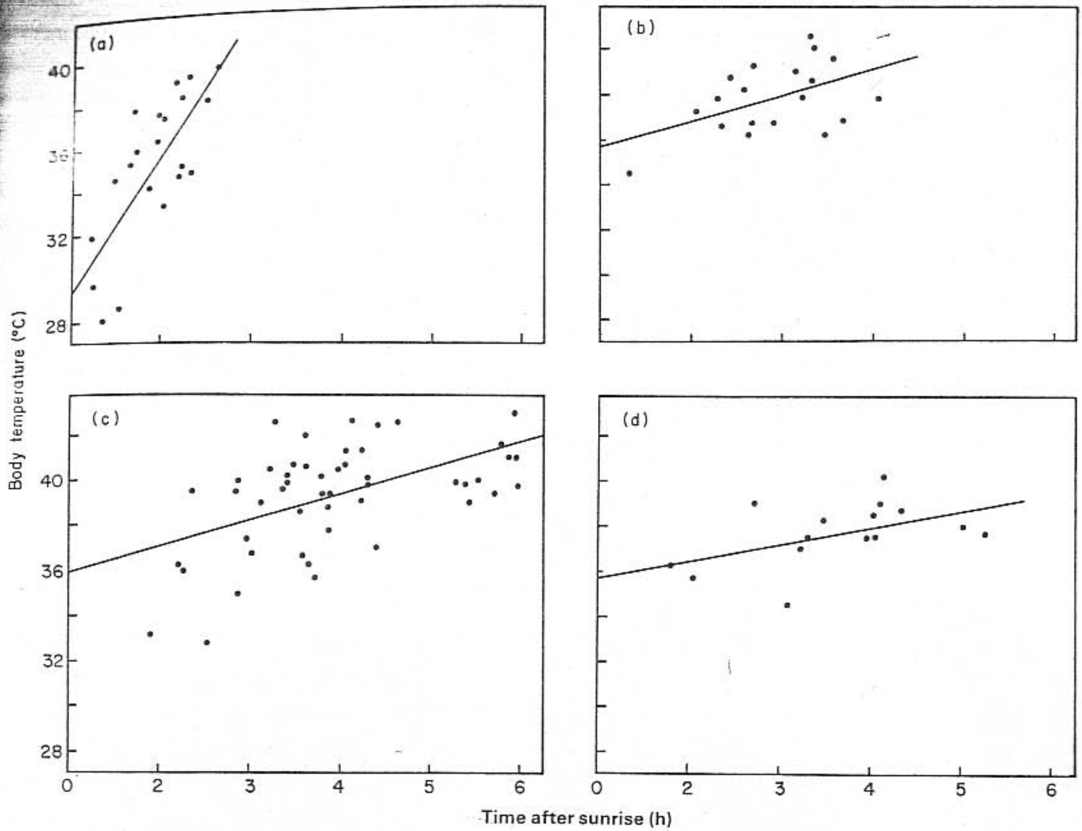

FIG. 3. Body temperatures of four diurnal lizards plotted against time after sunrise. (a) *Scincus mitranus;* (b) *Acanthodactylus schmidti;* (c) *Phrynocephalus arabicus;* (d) *Mesalina adramitana.*

Diet reflects foraging method to some extent. The two actively hunting species, *S. mitranus* and *A. schmidti,* take substantial volumes of beetles and insect larvae, animals that are usually not very apparent by day. The more passive forager, *P. arabicus,* on the other hand, eats a high proportion of flying insects and Orthoptera.

Body temperature and thermoregulation

Body temperatures of active animals are shown plotted against time after sunrise in Fig. 3. Overall means for each species and mean rates of temperature increase are given in Table III. On average, *S. mitranus* has the lowest body temperatures and *P. arabicus* the highest. These variations correspond to what is known about ecological differences between the species: the lowest temperatures are found in the one that emerges soonest after dawn, and the highest in that which is out latest in the morning and remains in hot, sunny situations for longest.

As might be expected from the relatively cool conditions in which it operates, *S. mitranus*

TABLE III

Temperature statistics for some diurnal lizards (based on morning activity period)

Species	n	Time of year	Body temperature (°C) Mean	Standard deviation	Average temperature rise per hour of activity (°C)
Scincus mitranus	21	Late April—early June	34·88	3·41	6·12
Acanthodactylus schmidti	19	Late April—early June	37·9	1·51	1·11
	21	Late March	36·81	1·12	
Phrynocephalus arabicus	49	Late April—early June	39·31	2·33	1·14
Mesalina adramitana	15	Late April—early June	37·69	1·43	0·74

seems to maximize heat uptake for most of its activity period, body temperature going up rapidly with time after dawn and the corresponding rise in intensity of insolation. The skinks observed spent much of their time hunting, and basking on eastwardly directed slip faces that were warmed by the rising sun and were 2–4°C warmer than surrounding flat areas. Body temperatures stopped close to that of the slip face, until they reached about 38°C, when the lizards ceased to bask and reduced heat uptake by moving into vegetation where they were shaded, or by digging so that their venters contacted cooler layers of sand that acted as a heat sink.

In the other two species, average body temperatures are higher but their ranges are less and their mean rates of increase lower. As the temperature of exposed ground rises much faster than that of the lizards during their activity period (see Fig. 1), they must be avoiding a substantial proportion of their potential heat uptake. In the case of *A. schmidti*, this appears to be done by utilizing shade thrown by the vegetation amongst which they live. Once they have reached their normal activity temperatures, these lizards spend a substantial proportion of their time wholly or partly in shadow, so that body temperature increases very little over the period of activity. *Phrynocephalus arabicus*, on the other hand, occupies very open shadeless situations where ground temperatures may exceed 50°C (indeed, Clark *et al.*, 1969 record the related *P. clarkorum* and *P. ornatus* on surfaces at 52°C and 59°C in Afghanistan). Heat uptake from the hot sand is reduced by the lizard keeping its body as far above it as possible by standing high on its legs. This will also expose the lizard to the wind, when present, which will increase forced convective cooling if the lizard is warmer than the air moving over it. Contact with the ground is minimized by the lizard resting only on the tips of its fingers and its heels, and the tail frequently touches the sand only at a single point, either about half-way along or at its tip. The spiny, downwardly directed scales on the underside of the feet reduce contact still further. This posture is only adopted once the lizard has reached its normal activity temperature range. Like other agamids in the area, *P. arabicus* is relatively dark above when it first emerges but becomes paler as it gets hotter. This increase in light reflectance should reduce energy input from the visible part of the solar spectrum. The permanently white venter may also be important in this way in limiting absorption of light reflected up from the sand. In addition, lizards cut down uptake of solar radiation by facing the sun, thus reducing the surface area exposed to it, indeed one species of *Phrynocephalus* has been named after this habit, *P. helioscopus*. Postural thermoregulation of the sort described here is common in desert agamids (Heatwole, 1976). Considering the heavy heat loads involved, it is remarkably efficient in controlling temperature.

Predator avoidance

Lizards that are active by day in open habitats in Arabia are subject to predation by snakes, monitor lizards and birds (especially shrikes and hawks), and the three species regularly found on soft sand have a number of adaptations that probably reduce the likelihood of being caught. Firstly, dorsal colouring matches ground colour very well. At Jebel Fayah lizards are reddish orange like the dunes at that locality, while at Sharjah 50 km away, they match the yellowish buff sand found there; 110 km from Jebel Fayah, on the whitish coastal dunes at Ras Ghanada, they become paler still. These differences are not transient, and *Scincus mitranus* in captivity for four years maintained their original colouring even when kept on contrasting backgrounds. Secondly, *Scincus mitranus* and *Acanthodactylus schmidti* both have fragile tails that break easily when grasped and can subsequently be regenerated.

Scincus mitranus appears to spend its resting hours in burrows with inconspicuous entrances close to the slip faces where it is active. However, it forages far from these refuges and, at such times, the principal means of escape is to dive rapidly below the sand surface. Animals on slip faces usually dive on the spot, over 82% of those observed did so within 0·5 m of where they were disturbed, and most within 0·2 m. Animals disturbed on firmer sand may also dive at once, but usually run to a slip face and, if approaching from its base, climb some way up it before diving. This is probably because sand on a slip face has recently been shifted by dune movement and is not closely packed, so that it is more easily penetrated than sand elsewhere. Probing faces with a metal rod indicates that the extent of such soft sand increases steadily from the foot to the crest; running upwards from the base consequently ensures there is enough for the lizard to bury itself completely. Slip faces also have the advantage that the sand is near its maximum angle of repose, and any attempt to dig the skink out will be impeded by causing sand to fall from above.

The skink enters the sand using its smooth, chisel-shaped snout. This is flat below but angled above, producing a downward turning motion that tends to direct the animal deeper into the sand, although this effect can presumably be counteracted by raising the head once the lizard is submerged. Progress through the sand is made easier by the narrow, streamlined head and foreparts, and by the smooth shiny skin. Initially, forward locomotion is provided by the limbs but, as these enter the sand, they are folded back against the flanks and the skink moves by vigorous lateral undulations, like a snake on the surface. Penetration is not usually very extensive, although skinks will dig deeper if touched. Animals that are dug up as soon as they have dived may have difficulty in re-burying themselves at once, especially if the process is repeated, when they often show signs of exhaustion. This suggests that sand diving is very energy consuming, which is not surprising given the density of the medium they travel through, and the fact that their cross-sectional area is great for their size, so that a large volume of sand has to be displaced. A more slender habitus, like that found in cryptic sand skinks such as *Sphenops* and some species of *Ophiomorus,* would allow more efficient burrowing, but would not be compatible with the adaptations of *Scincus* to active surface life. For instance, normal locomotion is accomplished almost entirely by the legs, the body often being held completely clear of the ground when running, something that would not be possible if the trunk were long and thin.

Pough (1969) has pointed out that lizards burying themselves in loose sand have a potential respiratory problem. In most forms, the sides of the thorax move inwards at each exhalation and, if an animal were submerged, sand would immediately fall into the gap thus created, preventing the expansion of the chest in inhalation. In most specialized loose-sand burrowers, this difficulty is avoided because respiratory movements are confined to the ventral wall of the thorax, so that gravity prevents the sand in contact with this area filling the space created by exhalation. Also, ventrolateral ridges may stop sand falling into this space from the sides, although it is unlikely that this is their only function for they extend well beyond the thoracic region to the hind limbs. It is possible that they make the flanks more vertical so that their efficiency in producing lateral thrust during sub-sand locomotion is increased.

Acanthodactylus schmidti, although also an active hunter, occupies less open habitats than *Scincus mitranus.* When disturbed, it often runs to vegetation where the complex filigree of cast shadows makes it inconspicuous. If pursued, it tends to dodge from bush to bush, but eventually takes refuge in systems of burrows that it digs at the foot of these. If an attempt to excavate these is made, the lizard may burst forth from the ground surface to run away again. Possibly, it has escape tunnels that approach, but do not quite break, the sand surface so a rapid and unexpected emergence can be made. This escape strategy is also reported for the Australian skink, *Egernia striata* (see Bustard, 1970). Distances fled to cover are often quite modest, but are usually further than the nearest clump of vegetation (Table I).

Phrynocephalus arabicus appears to be very dependent on crypsis for survival on the uniform sand surfaces where it forages. As stated, the colour match of its dorsal region with the substratum is good, and camouflage is enhanced by countershading and because its dorsoventrally flattened body reduces cast shadow. This lizard often seems to take up feeding positions near some small conspicuous object, such as an exposed root or dead leaf, which may distract the vision of a predator away from the far less conspicuous *Phrynocephalus.* Crypsis is further improved because the lizard remains motionless for long periods and movement is concentrated into short bursts of rapid locomotion and feeding. No formal experiments have been carried out on the importance of camouflage to these lizards, but an accidental observation suggests that its disruption may place them at a grave disadvantage. With the intention of getting some idea of home range size in *P. arabicus*, ten individuals were marked on the upper surface with one or two 3 mm diameter spots of bright pink, non-toxic paint. Each animal was restrained for, at most, 5 min and was released exactly where it was captured but, in spite of careful searching of the study area, only one was ever seen again. This was found spiked, shrike fashion, on a barbed-wire fence. As Great grey shrike (*Lanius excubitor*) was common, it may well have been the culprit. Six more lizards had been marked by toe clipping, which was unlikely to make them more conspicuous. Of these, at least three were still present 21 days later.

If pursued, *P. arabicus* often runs to the base of the nearest clump of plants and crouches, eliminating most of its own shadow. Alternatively, or if flushed again, the lizard may flee for quite long distances, running from plant to plant and often stopping very suddenly or changing direction very abruptly. If really hard pressed it will bury itself rapidly in the sand, frequently running out of sight behind a bush before doing so. Burial is not accomplished by diving head first into the sand as *Scincus mitranus* does; instead, *P. arabicus* flattens its body and oscillates it quickly from side to side, pushing sand over its back at each stroke, and sinks more or less vertically beneath the surface. The head and tail are buried by similar movements. The process leaves a distinct and, to human observers, characteristic mark on the sand, but presumably its significance escapes many predators. The distance run before burial is considerable, averaging 9·9 m for 32 cases.

While *A. schmidti* bites when captured, *S. mitranus* and *P. arabicus* in the United Arab Emirates do not, although the latter species does so in north west Arabia (J. Gasperetti, pers. comm.).

Diurnal lizards found on firmer sandy ground

Two species that have only been recorded a few times in the eastern United Arab Emirates are *Scincus scincus conirostris* and *Acanthodactylus boskianus.* They have been taken in habitats of consolidated sand interspersed with smaller areas of soft sand and, in some cases gravel as well. It seems likely that these species replace their congeners, *S. mitranus* and *A. schmidti,* on firmer, although not generally hard, surfaces. Some morphological features of *S. s. conirostris* support this. Unlike *S. mitranus,* its claws grow continuously if it is kept in captivity on soft sand, suggesting that they are normally worn down by more abrasive substrata. Adults, especially large males, lack the narrow very streamlined foreparts of *S. mitranus,* the head being large and broader than the neck and the snout tip less sharp-edged and chisel-shaped. This may indicate a lesser dependence on sand-diving for predator avoidance, something that is likely to be often difficult on harder substrata. Observations of this skink on firm ground on Bahrain suggest it may use permanent burrows as refuges (M. D. Gallagher, pers. comm.). In Dhofar, southern Oman, *A. boskianus* is found on harder ground than *A. schmidti* (softness 1–3, mean 1·6, $n = 42$).

Records for *S. s. conirostris* and *A. boskianus* in the United Arab Emirates come from a narrow band at the interface between the gravel plains, bordering the mountains and the areas of active sand dunes to the west. It is probable that their usual habitat is limited to this strip.

Diurnal lizards of harder ground

Three lizards are typically found on dry, relatively hard ground. These are the lacertid, *Mesalina adramitana* and the agamids, *Phrynocephalus maculatus* and *Agama flavimaculata.* In general, hard-ground species are less conspicuous and less abundant than those found on soft sand, and data for them are correspondingly sparser, although reasonable numbers of *M. adramitana* were observed. The overlap of this form with the common sand species in softness of ground occupied is very small (Table IV) and it is largely confined to gravel plain, fossil dune and consolidated sand, but in many other respects it is ecologically similar to *Acanthodactylus schmidti.* This applies to distance from vegetation at first sighting, time of morning activity, mean body temperature, distance fled to cover and the sort of refuges used. Like *A. schmidti, M. adramitana* adopts an active hunting strategy, scenting with its tongue and running in short dashes to search among stones, the interstices of bush-bases, under twigs and fallen leaves and even climbing in the lower branches of shrubs. Distances covered may be considerable and animals sometimes traversed 15 m in 5 min or so. However, on the basis of head and body size, prey is probably considerably smaller than in *A. schmidti.* In very warm conditions, *M. adramitana* may climb up grass stems to get off the hot ground surface. As with *A. schmidti, M. adramitana* often runs into the bases of shrubs when chased and may also use burrows that it digs itself, although this is less common than in *A. schmidti.*

TABLE IV
Niche overlap values for some diurnal lizards

Species pairs		Ground softness	Distance from vegetation (m)	Time after sunrise
Scincus mitranus	*Acanthodactylus schmidti*	0·245	0·543	0·528
Scincus mitranus	*Phrynocephalus arabicus*	0·221	0·855	0·147
Scincus mitranus	*Mesalina adramitana*	0·005	0·541	0·261
Acanthodactylus schmidti	*Phrynocephalus arabicus*	0·907	0·516	0·720
Acanthodactylus schmidti	*Mesalina adramitana*	0·172	0·999	0·654
Phrynocephalus arabicus	*Mesalina adramitana*	0·111	0·503	0·730

In two instances, lizards were seen uncovering the entries of burrows by removing loose earth before entering them. If nocturnal refuges are customarily blocked in this way, it explains why burrows are not frequently used by fleeing *Mesalina adramitana*, since opening them takes time. The purpose of burrow closure is uncertain, but it may prevent other lizards taking them over. This may be worthwhile because digging burrows in hard ground is costly in terms of time and energy. The process is much easier in soft sand and *A. schmidti* has the use of many open burrows.

Phrynocephalus maculatus behaves generally like a larger version of *P. arabicus* but occurs on sabkha, often partly covered with areas of thin sand, on gravel plains and on consolidated sand with gravel. Like its congener, it occupies open areas and hunts by sitting and waiting, and thermoregulates by posture and possibly by adopting pale coloration as it gets hotter. The relatively few animals seen tended to flee to bushes. Although this species is able to bury itself in loose sand as *P. arabicus* does, opportunities to do so must be limited in its usual range of habitats. *Phrynocephalus maculatus* will attempt to bite when restrained. Body temperature of a normally active adult male is 38·8°C.

Agama flavimaculata occurs on a variety of relatively hard substrata, typically with bushes, although these may be quite low. It is found on gravel plain, hard sand and alluvium and even areas of sandy sabkha. Animals are often seen early in the morning sitting on shrubs. Males at this time are blue with a red tail. *Agama flavimaculata* bites fiercely when handled. Temperatures of two normally active animals were 36·8 and 37·8°C.

Diurnal lizards from mesic habitats

Three diurnal species are more or less confined to usually rather moist habitats. *Pristurus rupestris* is a diminutive gecko that is widespread in the Oman mountains to the east of the area considered in this paper (Arnold & Gallagher, 1977), but in the lowlands it is restricted to relatively mesic areas that are often close to human habitation. An essentially "sit and wait" hunter, it is usually encountered on rocks, walls, the footings of buildings and even old car wrecks. Some aspects of its ecology in Dhofar, southern Oman are discussed elsewhere (Arnold, 1980*a*).

Mesalina brevirostris occurred as an isolated colony on the east side of the entrance to Sharjah creek. In many aspects of its ecology it is like the rather smaller *Mesalina adramitana* with which it is in contact, but *M. brevirostris* is confined to a moist area with succulent, halophytic vegetation near the sea, whereas *M. adramitana* occupies dry, more open areas further from the strand. All *M. brevirostris* observed were within about 6 m of the sea, compared with nine out of 55 *M. adramitana,* and 28 out of 34 were within 3 m, compared with six out of 55 *M. adramitana* (Differences significant at $P=0{\cdot}001$ level: χ^2 test).

Mesalina brevirostris is widespread in northern Arabia and also occurs on Bahrain, although at present it is recorded no closer to Sharjah than western Abu Dhabi. However, in these localities, it is smaller and less richly coloured than at Sharjah and occupies dry, more open habitats, just like *M. adramitana* which it at least partly replaces in these regions. It is not certain whether the *M. brevirostris* population at Sharjah is relictual or whether it is the result of accidental introduction from elsewhere. Temperatures of four specimens during the morning activity period were 32·5, 33, 37·5 and 39°C.

Chalcides ocellatus is a secretive skink found in plant litter and under other objects in plantations, amongst rubbish on the shore, and occasionally in gardens. It is typically encountered when searching among debris of various sorts, but is occasionally seen in the open.

Nocturnal lizards of widespread habitats

Lizards habitually active by night are abundant in the eastern United Arab Emirates and all belong to one family, the Gekkonidae. In contrast to some diurnal lizard communities, there is no evidence of species differences in times of activity and, in the spring at least, all forms become active around dusk and often remain so for some hours. Ecological separation appears to arise principally from differences in habitat and in prey size.

Seven species are associated with the widespread habitat types of soft sand, harder, often alluvial substrata and sabkha. These are *Stenodactylus doriae, S. leptocosymbotes, S. slevini, S. khobarensis S. arabicus, Bunopus tuberculatus* and *Teratoscincus scincus.* Some ecological parameters for most of these are compared in Table V.

Differences in microhabitat

The species of *Stenodactylus* all tend to occupy open areas between vegetation. The first four listed above are of fairly similar size in the United Arab Emirates but they are not usually strictly syntopic. *Stenodactylus doriae* is typically found on soft sand, although it avoids large slip faces, and forages well away from vegetation. *Stenodactylus leptocosymbotes* is encountered on consolidated sand or coarser alluvium. By and large, it occurs closer to shrubs and other plants than *S. doriae,* but this may merely reflect the greater abundance of vegetation on its preferred substrata. *Stenodactylus khobarensis* lives on ground that has scores for softness similar to that favoured by *S. doriae* but, instead of loose sand, it is confined to often moist sabkha. In this inhospitable habitat, where plants are often limited to the periphery, *S. khobarensis* is frequently seen a long way from vegetable cover. Observations in the United Arab Emirates and on Bahrain indicate that *S. slevini* lives in very similar habitats to *S. leptocosymbotes,* but the two species scarcely overlap and are essentially parapatric (Arnold, 1980*b*). They were encountered close together at only one locality in the United Arab Emirates, Ras Ghanada. West of here, only *S. slevini* appears to be found, while to the east it is replaced by *S. leptocosymbotes. Stenodactylus arabicus,*

TABLE V

Variation in some ecological parameters of nocturnal lizards. Entries are percentages of lizards observed

	Ground softness (see p. 332)								
	0–2	2–4	4–6	6–8	8–10	10–12	*n*	Mean	Niche breadth
Stenodactylus doriae	5·4	19·6	51·8	19·6	3·6		56	5·43	0·178
Stenodactylus leptocosymbotes	67·9	20·8	11·32				53	2·01	0·151
Stenodactylus khobarensis	7·9	21·0	60·5	10·5			38	5·11	0·192
Stenodactylus arabicus									
All	11·3	36·3	38·1	8·9	4·2	1·2	168	4·67	0·168
In habitats with *S. doriae*		20·5	57·5	12·5	8·2	1·4	73	6·43	
In habitats without *S. doriae*	24·2	46·3	27·4	2·1			95	3·61	
Bunopus tuberculatus	40·9	29·5	18·2	11·4			44	3·41	0·232
	Distance from vegetation when first seen (m)								
	0–0·5	0·5–1	1–2	2–5	5–10	10+	*n*	Mean	Niche breadth
Stenodactylus doriae	11·8	21·6	23·5	19·6	17·6	5·9	51	3·72	0·352
Stenodactylus leptocosymbotes	18·8	25·0	37·5	18·8			48	1·65	0·141
Stenodactylus khobarensis		12·9		22·6	54·8	9·7	31	7·39	0·183
Stenodactylus arabicus									
All	26·5	29·4	16·5	15·9	6·5	5·9	170	1·88	0·140
In habitats with *S. doriae*	12·0	20·0	22·7	18·7	14·7	12·0	75	4·43	
In habitats without *S. doriae*	37·9	36·8	11·6	13·7			95	1·25	
Bunopus tuberculatus	53·3	28·9	4·4	13·3			45	1·0	0·073

which is much smaller than the other species of *Stenodactylus* present in the area, often occurs alongside *S. doriae, S. leptocosymbotes, S. slevini* and *Bunopus tuberculatus*. As might be expected, it occupies a range of habitats. Where it was observed with *S. doriae*, it lived on soft sand with well-spaced plants and was frequently seen at substantial distances from these. In areas occupied by *S. leptocosymbotes* or *S. slevini* and places where *Bunopus tuberculatus* was dominant, *S. arabicus* occurred on harder substrata with denser vegetation, although it tended to occur in the spaces among this.

Bunopus tuberculatus also occupies a variety of habitats, being encountered in soft and harder sand areas. In contrast to *Stenodactylus* species, it is usually found closer to, or actually in, low shrubby vegetation, 82% of individuals being first sighted less than 1 m from such cover. Thus although it occurs with *S. doriae* in soft sand areas, *Bunopus* tends to be associated with the firmer sand in the vicinity of shrubs, while *S. doriae* occupies the more yielding ground between them. Similar, albeit less marked, separation is found in areas where *S. leptocosymbotes* and *S. slevini* occur. *Bunopus* also lives, in the absence of large *Stenodactylus* species, on quite firm substrata where there is a low, fairly continuous growth of such plants as *Cyperus arenarius* Retz., *Cornulaca arabica* Botsch, *Heliotropium kotschyi* (Bunge) Gürke, *Aeluropus lagopoides* (L.) Trin. ex Thw. and *Indigofera intricata* Boiss. It may, however, be accompanied here by *Stenodactylus arabicus*.

The few *Teratoscincus scincus* seen were on very fine sand with extensive, but scattered vegetation, such as *Artemesia* sp. Adults of this large form are probably able to take larger prey than any of the other nocturnal species.

Hunting techniques

Stenodactylus arabicus is largely a "sit and wait" hunter, like *Phrynocephalus* in Arabia. Animals stand or crouch with the head raised or resting on a slight eminence such as a sand ripple, and not infrequently face any breeze there is. From this position, they run forward to catch prey but are quite selective about this, not responding to many passing arthropods, especially if they are large. Foraging places may be retained for a few minutes (often about two to five) but are abandoned quite suddenly, the gecko running away, typically in a series of abrupt dashes, to take up a new position. In this way, it may cover 10–20 m in 30 min, often changing direction after each stop. The foraging behaviour of *S. khobarensis* is similar and both these species, which are probably quite closely related (Arnold, 1980*b*), often feed on very bare ground.

The other three *Stenodactylus* species may also forage from stationary positions, sitting or standing with the head raised. However, stations are often retained for longer, frequently 15 or 30 min at a time, and are not usually abandoned so precipitately. In addition, these geckos employ a technique that was not seen in *S. arabicus* and *S. khobarensis*. They walk very slowly with the legs fully extended for long distances. Following animals and the tracks that they make shows that over 200 m may be covered, the lizards keeping to open areas between shrubs. This behaviour occurs in a large number of ground-dwelling geckos, including *Teratoscincus scincus*, and it has been suggested that the very elevated locomotory posture enables them to see a long way over minor irregularities in the ground (Werner & Broza, 1969). Visually scanning the habitat for prey while slowly and continuously traversing it cannot be assigned to either of the two main lizard hunting strategies: "sit and wait" and active searching. As will be seen from Table VI, it shows a mixture of the characters of these two techniques, although it has more in common with active searching. Differences may stem partly from the fact that, in spite of often being nocturnal, geckos are very visual hunters, and do not seem to make so much use of aural and olfactory cues as active foragers like skinks and lacertids. Unlike these, slow visual scanners do not search for physically hidden prey. Their technique is likely to be particularly effective in finding prey that is exposed but does no travel far. It is uncertain why these visual scanners move so slowly, but there are at least two possible explanations, which are not necessarily mutually exclusive. Firstly, in poor light conditions, scanning the surroundings effectively may take time; furthermore, a slow scan, in which objects are given more than minimal attention, is likely to detect prey items that move only slowly or slightly. Secondly, in lizards hunting in open areas, slow movement may make them inconspicuous to visual hunters. Such a strategy is more likely to be effective by night. Certainly, diurnal ground geckos, such as *Pristurus* species, do not seem to engage in slow visual scanning. There are other forms that use this technique by day, such as chameleons, but these forage in complex, leafy environments that are likely to facilitate good crypsis.

Bunopus tuberculatus often forages by sitting and waiting, typically close to vegetation, or actually within its cover. This gecko may also hunt more actively within low shrubs, although how frequent this is is uncertain. It was never seen to walk slowly on fully extended

TABLE VI
Characteristics of some lizard hunting strategies

	"Sit and wait"	Active search	Slow visual scanning
Main sensory systems involved	Vision	Vision, hearing, olfaction	Vision
Vulnerability to visual predators	Low because lizard mainly immobile and can therefore forage in exposed positions if crypsis good	High because lizard mobile; therefore, unless predators absent, active search is only likely to take place in protected situations, e.g. in or close to cover	Quite high
Energy cost and necessary prey abundance	Cost low because lizard largely immobile; may therefore be feasible even when prey sparse	Cost higher because lizard active; prey abundance must therefore be relatively high	Intermediate
Prey mobility	Must be high to reach lizard	Can be very low	Can be low
Prey visibility	High, prey often detected at considerable distance	May be very low; hidden prey often detected	Relatively high
Prey distribution in space		May be very irregular	May be very irregular
Prey distribution in time	May be very irregular		
Human analogy when hunting small animals	Shooting passing animals from inconspicuous, stationary position	Finding cryptic forms by turning stones, searching litter, beating bushes etc.	Walking slowly and scanning rock faces, tree boles etc. for exposed forms with small home ranges

legs, something that its congener, *Bunopus spatalurus*, a species of more open habitats, does (Arnold & Gallagher, 1977). Animals were also occasionally seen in the entrances of rodent burrows, so it is not impossible that they also forage below ground.

Diet

No detailed study of diet was made, but examination of small series of stomach contents indicates that the geckos discussed here all eat a wide variety of invertebrates, most of which are arthropods, especially insects. Differences appear to reflect variation in the availability of prey types in particular habitats. Prey size shows a rough correlation with the dimensions of the lizards concerned, particularly the size of the head. This being so, it is unlikely that *S. arabicus*, which is much smaller than the other species with which it coexists, competes significantly for food with them. Its maximum head dimensions are far smaller than those of all except the most juvenile individuals of the other forms. There may also be a less clear differential in prey size between adults of the large *Stenodactylus* species and the rather smaller *Bunopus tuberculatus*.

Body temperature and thermoregulation

The following body temperatures were recorded for naturally active *Stenodactylus*.
S. doriae: $n=17$; range 23·5 – 30°C; mean 28·24°C; standard deviation 1·9°C;
S. leptocosymbotes: $n=8$; range 24·5 – 28·5°C; mean 26·75°C; standard deviation 1·15°C;
S. khobarensis: $n=3$; 29·5, 30, 30·5°C.

These temperatures were all within 1·8°C of ambient and suggest that the geckos are active close to the temperature of their immediate surroundings. No direct temperatures were taken of *S. arabicus* because of its very small size, but it too is likely to operate at ambient temperatures; these varied from 21 to 30°C.

Temperatures of *Bunopus tuberculatus* have been discussed elsewhere (Arnold, 1980*a*). Those of 20 animals active after dark ranged from 26 to 34°C. Most were close to the ambient but six exceeded it substantially, with differences of 2, 4·5, 4·5, 4·5, 5 and 8°C, something that was not encountered in other nocturnal geckos. As already noted, *Bunopus tuberculatus* is sometimes seen in the entrances of rodent burrows at night and it may possibly descend these to lower levels where heat is retained in the soil. Alternatively, geckos in this situation may be heated by up-draughts rising from the burrows. This species seems to select warm micro-habitats during the day as well. Six animals excavated from burrows were all in sections of tunnel very close to the sun-warmed surface of the ground. Their temperatures were 33·4, 35·5, 35·5, 36·5, 37 and 37°C, much higher than the air temperature at lower levels in the burrows.

Predator avoidance

As with diurnal species, the dorsal pattern of ground geckos matches their background quite closely and, from above, they are not very conspicuous. All have the capacity to shed the tail if a predator makes contact with it. In *Stenodactylus doriae, S. leptocosymbotes* and *S. slevini* such caudal autotomy takes place only at the base but, in the other species, it can occur at virtually any point in the tail. Some forms, such as *S. arabicus,* have conspicuously marked tails, and move them in a way that may divert the attention of a predator from the more vulnerable head and body. *Teratoscincus scincus* also moves its tail in the presence of danger, in slow lateral sinusoidal waves, and especially modified scales on its upper surface produce a hissing noise. In this species, large areas of the body skin may be shed if the lizard is grasped (Minton, 1966; Arnold, 1977).

It is probable that all the ground geckos spend their resting hours in burrows, although these are usually only found if they happen to be under some movable object. *Stenodactylus arabicus, S. khobarensis, S. leptocosymbotes* and *S. slevini* have all been discovered in such refuges, which are usually quite short and shallow. The geckos appear to excavate the burrows themselves, and this is certainly true of the *Stenodactylus* species listed above. A *S. arabicus* was seen to dig open the closed entrance of a burrow and go inside, like the *Mesalina adramitana* mentioned on p. 342. Although *Bunopus tuberculatus* probably makes its own burrows, these often commence in the burrow systems of rodents.

The species of *Stenodactylus* show considerable variation in their response to being approached. *Stenodactylus khobarensis* is an efficient escaper, running fast to take refuge in often halophytic vegetation. Although rather less adept at evading capture, *S. arabicus* will also flee into dense low plants but, in open areas, will frequently run in a series of dashes with abrupt stops and may change direction in between them. *Stenodactylus doriae* and *S.*

leptocosymbotes are not as fast as the foregoing species but they run quite swiftly to crouch close to shrubs, although they do not enter them. Alternatively, they dash about in an uncoordinated manner which may possibly arise from being dazzled by the observer's lamp. *Bunopus* is like *S. khobarensis* and *S. arabicus* in running immediately into dense vegetation when this is available. At least *Stenodactylus doriae* and *Bunopus* may bite if captured.

Nocturnal lizards of more mesic habitats

Three further species of nocturnal geckos are associated with more mesic habitats than the species described above, and often with areas of human activity, particularly when these are irrigated.

Cyrtodactylus scaber is superficially like *Bunopus tuberculatus* and probably resembles it in many aspects of its ecology, but it lives in moist places: irrigated gardens, rubbish dumps, areas of sand and rocks close to the sea, footings of buildings etc. Also, unlike *Bunopus*, it climbs on rocks and walls, although not usually extending far upwards, most records being less than 0·5 m from the ground. When disturbed, it runs rapidly to hide in holes or vegetation.

Hemidactylus turcicus parkeri is more scansorial, and may be encountered on the insides and outsides of buildings and on tree boles and fence posts in and around plantations. But it also sometimes occurs on the ground, and may be found in rubbish piles, under heaps of old matting and in discarded palm fibre, although it seems to prefer hard surfaces. Where *H. turcicus* is found with the rather larger *Cyrtodactylus scaber*, it climbs more and to greater heights. Near Sharjah, it was observed with *Bunopus tuberculatus* in an ecotonal area, but while the latter occupied the flatter more sandy places, *H. turcicus* was mainly associated with rocks, well heads and small vertical faces, from which it came down to forage.

The third species, *Hemidactylus flaviviridis*, is larger than *H. turcicus*, more strictly scansorial and climbs higher. Twenty eight out of 30 checked were over 2·1 m from the ground compared with 10 out of 61 *Hemidactylus turcicus*. *Hemidactylus flaviviridis* occurs on the inside and outside of buildings, on the boles of palm trees and on fence posts and telegraph poles.

Critical maximum temperatures

Freshly caught individuals of several species were exposed to the midday sun without access to shade. After their normal activity temperatures were exceeded, they usually panted and, with further temperature rise, collapsed and were unable to right themselves when placed on their backs. At this point their cloacal temperatures were recorded as a rough indication of the level at which they ceased to be able to function effectively. In natural conditions, death would rapidly supervene, but all experimental animals recovered completely on being cooled immediately after their temperatures were taken. Critical maximum temperatures obtained in this way were as follows.

Scincus mitranus: 46·8, 47°C;
Acanthodactylus schmidti: 41·3, 43·3, 44·3°C;
Phrynocephalus arabicus: males 47, 47·7, 48·5, 48·5°C (mean 47·9°C); females 45·1, 45·2, 45·2, 45·2, 46·5, 46·5, 46·9, 47°C (mean 46°C);
Mesalina adramitana: 46·3°C;

Stenodactylus doriae: 40·5, 43·5°C;
Bunopus tuberculatus: 41, 45·2°C.

All these temperatures are well above the normal spring activity range of the species concerned (Table III). This contrasts with, for instance, the North American desert iguanid, *Dipsosaurus dorsalis*, whose habitat activity temperatures are very close to the upper physiological limit of the animal (Dawson, 1975). On the basis of relatively few individuals, the critical maximum temperatures of *Phrynocephalus arabicus* appear to be especially high and to show sexual dimorphism, those of males being almost 2°C higher on average than females ($P = 0{\cdot}01$, Student's *t*-test).

Reproduction

The majority of the species discussed are oviparous, although no information exists for the skink populations in eastern Arabia. However, *Chalcides ocellatus* gives birth to fully developed young in other areas and is consequently likely to do so here. *Scincus scincus scincus* lays eggs in Egypt (Badir & Hussein, 1965), so *S. s. conirostris* may do so as well.

Available information on likely clutch size, based on number of oviducal eggs carried, and the dates when these are present are given in Table VII, which also contains information on some species from the mountainous parts of the United Arab Emirates. It will be seen that probable clutch size shows substantial correlation with body size. Thus the smallest species, *Pristurus rupestris* and *Stenodactylus arabicus,* always lay single eggs, whereas comparatively large forms such as *Agama flavimaculata, A. sinaita* and *Teratoscincus scincus* may bear four or more. The relatively small *Mesalina* species could be an exception to this trend as up to four eggs may be carried.

Many species show intraspecific variation in oviducal egg number. In species laying either one or two eggs, number does not seem to correlate with body size or season, on the evidence of the small samples available, although this may not apply to the larger forms. Within the Gekkonidae, the number of eggs in a clutch, either one or two, has been used as a taxonomic character (Kluge, 1967) but data in Table VII suggest this feature is very plastic, for six species of three genera may produce either one or two eggs. Most egg carrying takes place in the spring, and the majority of records are for late March, April and May, although earlier ones exist for such species as *Acanthodactylus schmidti, Mesalina adramitana, Agama sinaita* and *Stenodactylus doriae.* For many forms, dates of egg carrying are spread over two months or more, suggesting that breeding is repetitive, a number of clutches being laid. The few records of the appearance of hatchlings that exist indicate that, as might be expected, many young appear in late spring and summer.

Little information exists on the time taken to reach maturity, but in some of the smaller species it is probably under a year. *Acanthodactylus schmidti, Phrynocephalus arabicus* and *Stenodactylus arabicus* are common as adults in the spring, but virtually no juveniles are present until eggs laid that year hatch, so these presumably reach full size by the next spring.

Tail autotomy

Among lizards present in eastern Arabia, all members of the families Scincidae, Lacertidae and Gekkonidae can autotomize and regrow the tail. Broken and regenerated tails are generally commoner in climbing species than in ground dwelling ones. This relationship

TABLE VII

Body size, clutch size and time of reproduction, based on material from the United Arab Emirates. Some species from the eastern mountains are also included and distinguished by asterisks

	Usual maximum snout-vent length (mm)	Clutch size based on number of oviducal eggs (entries indicate number of females)							Time of year when oviducal eggs encountered (by half months, entries indicate number of females)											
		1	2	3	4	5	6	7	Jan		Feb		Mar		Apr		May		Jun	
Chalcides ocellatus	100																			
Scincus s. conirostris	100																			
Scincus mitranus	120																			
Acanthodactylus schmidti	63	7	3						1					5	1		1	2		
Mesalina adramitana	42		2	1	1					1		1						1		
Mesalina brevirostris	55				1											1				
Agama flavimaculata	130			1				2												
*Agama sinaita**	85				3								1	1			1			
Phrynocephalus arabicus	46	6	11											1			1		1	
Phrynocephalus maculatus	65		1																	
Uromastyx microlepis	200+																			
Varanus griseus	300+																			
*Bunopus spatalurus**	50	5	6											5	1	1	1	1		1
Bunopus tuberculatus	50	7	11													3	6	3		
Cyrtodactylus scaber	50		7														2	2		1
Hemidactylus flaviviridis	90	2	2												1	1				
Hemidactylus turcicus parkeri	50		4										1		1			1		
*Phyllodactylus elisae**	63	2												1			1			
*Pristurus celerrimus**	37	1							1											
Pristurus rupestris	30	11												3	6	1				
*Ptyodactylus hasselquistii**	90		5														4	1		
Stenodactylus arabicus	37	18															15	3		
Stenodactylus doriae	65	1	7						1					1			1	1		
Stenodactylus khobarensis	53	3	4												1	2		1	2	
Stenodactylus leptocosymbotes	62		4											1			2	1		
Stenodactylus slevini	57	2	2																	
Teratoscincus scincus	120																			

has been noted in Palestinian geckos (Werner, 1968) and is also found in European lacertids and African *Agama*. Incidences of naturally autotomized tails among adults of species from the lowland and mountain regions of the United Arab Emirates, based on material in the British Museum (Natural History), are reported elsewhere and their possible significance discussed (Arnold, 1984).

Morphological correlates with niche

Body shape and usual feeding and escape behaviour

Among the diurnal lizards, the agamid "sit and wait" foragers all have short, plump bodies, short squat heads and relatively long legs, whereas the actively hunting varanids, skinks and lacertids are longer bodied with narrower heads and usually shorter legs. It seems probable that the second body type is efficient for passing through vegetation and hunting in restricted places, but is not necessary in species that forage predominantly in open spaces. The same trends are present, although less marked, in ground geckos: *Bunopus tuberculatus* which usually lives in and around vegetation is longer bodied and shorter limbed than many of the *Stenodactylus* species that hunt in open areas, especially compared with those that forage by walking slowly on extended legs. Vitt & Congdon (1978) demonstrate that the "sit and wait" body shape is correlated with a larger relative clutch mass.

Body shape also shows an association with the methods of escape usually employed. Forms that often resort to fleeing into dense vegetation and bush bases, or, in the case of *Scincus,* to sand diving, are relatively long bodied and short limbed compared with those that do not. Examples of the first type are *Acanthodactylus, Mesalina, Chalcides, Bunopus, Cyrtodactylus, Stenodactylus arabicus* and *S. khobarensis.* All these are much more slender than *Phrynocephalus, Stenodactylus doriae, S. leptocosymbotes* and *S. slevini,* which may run to the perimeter of shrubs but typically avoid entering them deeply. Also, although *Phrynocephalus* buries itself, it does not dive head-first into the sand like *Scincus,* but digs down vertically.

Foot structure and substratum

Virtually all the ground-dwelling forms regularly encountered on hard substrata have simple cylindrical digits, while those habitually living on soft sand have depressed digits with lateral fringes of flattened, often elongated, pointed scales. These occur in *Scincus, Acanthodactylus, Phrynocephalus, Stenodactylus doriae, S. arabicus* and *Teratoscincus scincus.* Digital fringes act like snow shoes in increasing the spread of the feet so that weight is distributed over a larger area of the yielding substratum, preventing sinking and giving better purchase in locomotion and digging. In general, the length of the scales making up digital fringes correlates with the softness of the sand occupied. Thus, they are longer in *Scincus mitranus* and *Acanthodactylus schmidti* than in their congeners from firmer substrata, *S. scincus conirostris* and *A. boskianus*. At first sight, *Stenodactylus arabicus* is anomalous in this respect. In spite of its small size and lightness, it has well developed fringes and extensive webbing between the toes as well, yet the apparent mean softness of the ground it lives on is considerably less than that occupied by other species with fringes, and it frequently occurs on quite firm surfaces with average measured softnesses of only 3·6 (see Tables I and V). However, this discrepancy may be at least partly an artifact of the rather crude method used to assess ground softness (p. 332). High readings are only obtained if the ground is soft to a depth of some centimetres. A hard surface covered by a thin layer of fine, soft sand is consequently interpreted as hard, yet for a minute lizard like *S. arabicus* such a layer could still impede progress, making lateral fringes and webbing advantageous. Certainly, on ostensibly hard substrata, it frequently occurs on tiny drifts of soft sand overlying the firmer ground beneath.

Stenodactylus khobarensis has peculiar swollen digits covered below by an array of sharp spines. This means that, when standing on sabkha, the lizard contacts the sticky granules of its surface only at a number of very restricted points. The area of contact is consequently low and particles do not adhere to the feet. In contrast, the toes of other *Stenodactylus* species kept in captivity on moist evaporites from sabkha soon become heavily caked.

Scansorial species also have characteristic foot structures that assist climbing, such as the digital compression and kinking found in *Cyrtodactylus scaber* and *Pristurus rupestris* and the adhesive pads present in *Hemidactylus.*

Adaptations to sandy environments

In addition to modified feet, lizards living in soft sand habitats often possess a range of adaptations to this environment. In particular, there are a number of devices that keep sand out of the body, including nasal valves, long nasal passages that probably act as gravity traps, countersunk jaws and fringes of long scales on the edges of the eyelids that keep sand away from the cornea (see Stebbins, 1944). All, or most of these features are well developed in *Scincus, Acanthodactylus* and *Phrynocephalus*. The forms habitually burying themselves in loose sand have the external ear opening greatly reduced (*Scincus*), or absent (*Phrynocephalus*), and the columella auris may be robust. These features probably reduce the sensitivity of the ear to airborne sound, but may make it more suitable for detecting vibration transmitted through the ground.

Comparison with other parts of the Saharo-Arabian desert area

Most of the species found in relatively mesic habitats in the eastern United Arab Emirates are only distributed peripherally in the rest of the Arabian peninsula, and are absent from the arid centre. This applies to *Chalcides ocellatus, Pristurus rupestris, Cyrtodactylus scaber, Hemidactylus turcicus* and *H. flaviviridis.* Two other forms discussed here also have a restricted distribution in Arabia: *Stenodactylus khobarensis,* known only from the south and west coasts of the Arabian Gulf, and *Teratoscincus scincus,* confined to the south coast of the Gulf, although it has a wide range in east Iran, Pakistan and central Asia. The remaining lizards, which are found in arid habitats in the United Arab Emirates, are broadly distributed across much of Arabia, but some of them are replaced by similar forms in certain areas. This fauna extends almost intact through inland Oman to northern Dhofar and Hadhramaut. Most species reach the inland face of the southwestern mountains of the peninsula, although *Mesalina adramitana* is replaced by *M. guttulata* and *Stenodactylus leptocosymbotes* by *S. slevini*. These forms also occur in north-east Arabia where *Mesalina brevirostris* is widespread and *Agama flavimaculata* is replaced by *A. blanfordii*. In the north-west, *Scincus scincus conirostris* and to a large extent *S. mitranus*, are replaced by *S. scincus meccensis* and again *M. guttulata* and *Stenodactylus slevini* are found. In the north of Arabia some other additional species appear, such as the largely ground-dwelling *Agama pallida* and another sand-living *Acanthodactylus, A. scutellatus hardyi.* Where it is sympatric with this relatively small species, *A. schmidti* is very large; this may be an example of character displacement (Arnold, 1981).

Coastal south-west Arabia

This area consists of a narrow strip of arid lowland habitats in Asir and North and South Yemen that is largely separated by mountains from the inland deserts of Arabia, and has a markedly different fauna from them. *Acanthodactylus schmidti* is replaced by *A. arabicus* and, from Asir to the Aden region, the *Stenodactylus* found on firm ground is *S. yemenensis.*

Here, no soft-sand *Stenodactylus* has yet been reported, and the niche usually occupied by *S. doriae* may be at least partly filled by the largely nocturnal skink, *Scincus hemprichii.* Whether this skink also partly occupies the ecological space filled by *S. mitranus* elsewhere in southern Arabia is unknown. At least one *Mesalina* (*M. guttulata*), *Agama flavimaculata* and *Bunopus tuberculatus* are all present, but *Phrynocephalus* is unknown. Its place may be at least partly taken by a gecko of the *Pristurus carteri* complex, for elsewhere in south Arabia this lizard resembles *Phrynocephalus* ecologically (Arnold, 1980*a*). Further to the east, south of the Hadramaut, *Stenodactylus pulcher* is found. This relative of *S. arabicus* has strongly fringed toes and is consequently likely to occupy relatively soft sand.

The Sahara

The Sahara has many of the genera found in the desert areas of Arabia including *Scincus, Acanthodactylus, Mesalina, Agama, Uromastyx, Varanus* and *Stenodactylus,* as well as a number not encountered to the east, such as *Sphenops* and *Scincopus.* Widespread species of the shared genera seem to fill similar niches to their congeners in Arabia, but some Arabian elements are missing. Thus there are no *Phrynocephalus* and no *Bunopus.* In the case of *Phrynocephalus,* there seems to be no obvious analogue in soft-sand habitats. Diurnal soft-sand species in the Sahara include members of *Scincus* and *Acanthodactylus,* but nothing that looks likely to fill the niche occupied by *P. arabicus.* Given the similarity between Arabian and Saharan habitats and many of their occupants, it seems probable that there would be ecological room for *Phrynocephalus,* especially as its niche is well differentiated: in Arabia it overlaps very little with *Scincus* in ground hardness, time of activity and feeding strategy, or with *Acanthodactylus* in feeding strategy and openness of habitat occupied. One possible explanation is that *Phrynocephalus* may never have had the opportunity of invading the Sahara. Like *Bunopus* and *Teratoscincus,* it is a genus with most species in Iran and central Asia, a region that is zoogeographically very distinct from Arabia. Representation in the latter area is poor: *Teratoscincus* has only a single non-endemic species and *Phrynocephalus* and *Bunopus* have one endemic and one non-endemic species each. This poor representation may indicate that all three genera are relatively recent immigrants into Arabia. If this is so, their failure to penetrate into the Sahara across Wadi Arava (which coincides with the range limits of many species), or into the isolated coastal south-west of Arabia, is more understandable.

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