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The European bee-eater (*Merops apiaster*) as an ecosystem engineer in arid environments

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Abstract

Arid environments are fragile ecosystems where management is particularly complicated. Determining target species that contribute to understanding the functioning of such environments is of basic importance. Here we assess the role of the European bee-eater, a burrow-nesting bird species, as an ecosystem engineer in arid ecosystems. We conclude that this species may play an important function in basic abiotic and biotic processes of arid environments since: (i) it can be a major bioturbating organism in arid areas, removing a noticeable amount of soil and making it more sensitive to climatic factors, (ii) it enhances biodiversity by providing nesting and roosting habitats to a broad array of organisms, and (iii) it provides resources (food) to many other species, thus reinforcing the structure of the community and enhancing more complex food webs.

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1. Introduction

Arid and semi-arid zones are fragile ecosystems that merit special attention. As with many other environments, two main aspects should be considered to keep this system healthy: conservation of soil and water as a key process and maintenance of

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biodiversity and productivity as important functions of healthy ecosystems. The vulnerability of arid and semi-arid Mediterranean regions to erosion and desertification can lead to rapid and intense destruction of the soils (Lopez-Bermudez and Romero-Diaz, 1989). This, in turn, influences biodiversity and productivity. Thus, efficient management and conservation policies are required in arid ecosystems. Because monitoring and managing all aspects of biodiversity are difficult, it has been proposed to focus our attention on one or a few species with specific, potentially valuable characteristics (Simberloff, 1998). One of such species type is the so-called keystone species (Bond, 1993; Paine, 1995). A keystone species is an organism with a significant influence on the ecosystem it occupies that is disproportionately large compared to its abundance or biomass (Simberloff, 1998). Keystone species are functionally linked to the persistence of an array of other species and play a critical role in the organization and/or functioning of the ecosystem. Mills et al. (1993) described five broad categories of keystone species, one of them being keystone habitat modifiers, also called ‘ecosystem engineers’ (Lawton and Jones, 1995). Physical ecosystem engineers are organisms that create, modify or maintain habitats by causing physical state changes in biotic and abiotic materials that, directly or indirectly, modulate the availability of resources to other species (Jones et al., 1994, 1997). Whereas not all engineers are keystone species (Jones et al., 1997), Wilby (2002) proposed that the term ‘ecosystem engineering’ can also be used to describe the activities of those organisms whose action creates or modifies habitats although they are not influential enough to be ecosystem engineers.

The European bee-eater is a widely distributed species, although mainly locally abundant, in arid and semi-arid areas (Cramp, 1985) where it usually selects sandy cliffs in wadis. It is one of the few bird species with the ability to modify the habitat by digging long burrows where it breeds, therefore fitting to the definition of allogenic engineer proposed by Jones et al. (1994). This ability could be important because it gives it some potential as an erosive agent (i.e. bioturbator) and because it may enhance biodiversity by providing basic resources (e.g. habitat) for other species. In this study, we assess the importance of the European bee-eater as an ecosystem engineer and examine its ecological role in semi-arid environments in south Spain by evaluating: (i) its erosive potential, (ii) the consequences of habitat modification from the perspective of biodiversity, (iii) its role enhancing interspecific interactions structuring the community.

2. Materials and methods

2.1. Study area

The main study site was located at the Desert of Tabernas (Almería, South-east Spain, 37°05'N, 2°21'W). In this locality, a colony of bee-eaters located in a sandy cliff approximately 100 m long and 3–5 m high was studied during 2000–2002. Bee-eaters have been breeding in this cliff for years, with fluctuating numbers: during

2000, 40 pairs bred in the colony, 25 in 2001 and 2 pairs in 2002. Currently the cliff has approximately 500 burrow-nests.

Climate in this area is semi-arid with long hot summers, strong fluctuations of temperature both on a daily and seasonal basis, and high annual and seasonal variability of rainfall (annual average 218 mm) (Puigdefábregas et al., 1996). Soil is weakly developed, unconsolidated and with low erosional resistance. As a result, this area, and in general the whole landscape of South-east Spain, constitutes a fragile environment where erosional processes are rapid and the destruction of the soils is very intense (Lopez-Bermudez and Romero-Diaz, 1989).

A second colony located in Puertollano (Ciudad Real, 38°42'N, 4°07'W), 240 km north-west from our main study site, was studied during 2000. In this location the study was restricted to sampling old bee-eater nests looking for invertebrates. Climate in this area is continental, with an annual average rainfall of 560 mm (Capel, 1981).

2.2. Study species

Bee-eaters are migrant, colonial, aerial insectivorous birds which nest in cavities at the end of deep burrows (Cramp, 1985) mainly in vertical or very sloped cliffs. Bee-eaters usually dig a nest every breeding season (Cramp, 1985) although they can also reuse old nests (Cramp, 1985). In our study area nest reuse is rare. Before selecting a final nest site, they often excavate 2–3 cavity starts to as much as 60 cm before concentrating solely on eventual nest hole (Cramp, 1985). Thus cavity starts can be found in various stages of completion; several may have dimensions similar to active nest cavities and others, though not as large, can be deep enough to function as potential nesting or roosting habitat for some other species (pers. obs.).

2.3. Estimating bioturbation ability

The erosive effect of bee-eaters is two-fold: (i) they actively remove soil when digging deep burrows to nest, (ii) a secondary effect of such activity is that burrows weaken the cliff and some parts collapse as a consequence of mining (see below). Therefore, to estimate the importance of bee-eaters as erosive agents (bioturbators), we calculated in our study area: (i) the amount of material removed directly by the bee-eaters during nest building for three years (2000, 2001 and 2002), and (ii) the volume and weight of the collapsed pieces during this time.

Estimating the amount of sand removed by a pair of bee-eaters requires the calculation of the volume of a nest. The nest of the bee-eater is an excavated tunnel ending in an enlarged breeding chamber. We approximated the tunnel as a cylinder and, thus, we calculated the volume using the formula:

$$V = \pi R^2 H,$$

where R is the radius and H the height.

Concerning the breeding chamber, we considered it an oval-shaped space and thus we calculated its volume following the formula:

$$V = \frac{4}{3}\pi R_1 R_2 R_3,$$

where R_i are the three perpendicular radii.

Data needed to calculate the volume were taken from nests in our study area and from the literature. During the 2001 breeding season we measured the length of 18 nests, obtaining a mean value of 142.8 cm (95% confidence interval: 132.9–152.7 cm). Only nests where we were able to reach the breeding chamber were used for this calculation. Our estimation is similar to the ones cited elsewhere (see, for instance, Kossenko and Fry, 1998). The measurements of the diameter of the tunnel and of the chamber were taken from Cramp (1985), being 6.5 cm and $32 \times 25 \times 12$ cm, respectively. When calculating the volume of the tunnel we considered its length minus the length of the breeding chamber.

Our estimation of the bioturbation ability of bee-eaters is conservative because: (i) we did not include the volume excavated for cavity starts. In our study area bee-eaters seldom dig cavity starts and when doing so, they are not very deep (less than 20 cm). However, other studies report that pairs routinely dig several long cavity starts (Cramp, 1985; Ar and Piontkewitz, 1992), (ii) the average volume of the nests in our study area seems to be lower than the one reported for nests in other areas. Ar and Piontkewitz (1992) estimated an average volume (\pm S.D.) of 21.7 ± 8.81 (ca. 2.4 times larger) for bee-eaters nests built in the coastal plain of Israel.

Collapse of several parts of the sandy cliff was observed during the study period. Climatic factors (e.g. rain) are certainly partly responsible of such collapses but we believe that they would not occur if the cliff was not weakened by hundreds of burrows. Therefore, we assume that the ultimate factor accounting for collapses is bee-eaters' mining activity. Collapses recorded during these 3 years are probably the consequence of bee-eater nests built both during the study period but also during previous years. We measured the collapsed pieces and estimated their volume by approximating their shape as regular prisms.

Mass of excavated soil and of collapsed pieces was calculated by multiplying the estimated volume by the soil density, that in our study area is $1.486 \text{ kg l}^{-1} \pm 0.032$ S.E. (95% confidence interval: 1.417–1.555) (Puigdefábregas et al., 1996).

2.4. Bee-eater nests as habitat for other species

Data on vertebrates using bee-eater nests come from our study area, reports from experts and ornithologists and from a literature survey. We also sampled invertebrates from bee-eater nests used by secondary-cavity-nester species (e.g. Rock sparrow *Petronia petronia*) and bee-eaters by taking nest material (straws, sand) during the nestling phase or the whole nest soon after (maximum 6 days) the nestlings fledged, and we collected darkling beetles that were observed climbing the cliff and entering bee-eater nests.

A survey of invertebrates using old bee-eater nests was done in the colony located at Puertollano. Entomological chromatic traps (cardboard with glue on both sides

and measuring 6×5 cm) were located at the entrance (ca. 10 cm inside the tunnel) of 33 bee-eater nests used in previous seasons (see Valera et al., 2003 for more details) at the beginning of May and collected 1 month later. Fresh traps were then placed again and taken back 45 days later. These results cannot be extrapolated to arid areas but they provide an overall idea about the invertebrate fauna using bee-eater nests.

3. Results

3.1. Bioturbation ability

The average volume of sand excavated during the construction of a nest amounts to 8.711 that equals 12.94 kg (95% confidence interval: 12.34–13.54 kg). In our colony no breeding pair reused old nests and all nests were excavated on the cliff. Sixty-seven nests were dug during the 3 study years, which amounts to ca. 5831 or 867 kg (95% confidence interval: 826.8–907.2 kg) during three breeding seasons.

During the study period four large pieces collapsed from the cliff, amounting to 30641 or 4554 kg (95% confidence interval: 4342.2–4765.1). These estimations do not include small, difficult to measure, pieces that fell down with the large ones or in other moments.

3.2. Bee-eaters as suppliers of resources for other species

In our study area we recorded six bird species nesting in old bee-eater nests. Some of them (e.g. sparrows) just needed to add some nest material into the old burrows. Enlargement of old bee-eater nests by erosion (piping) and by active digging of secondary nesters made old burrows available for larger species (e.g. European roller *Coracias garrulus*, Little owl *Athene noctua*). We gathered information about another six bird species nesting in old bee-eater nests (Table 1). Whereas nest reuse by some species (Pied wagtail *Motacilla alba*) can be occasional, other birds frequently reuse bee-eater nests. In our study area the most favoured species was the Rock sparrow, with a maximum of 100 breeding pairs in 2000 and 2001.

In contrast to birds, other vertebrate species occupying old bee-eater nests use them as shelter or roosting places. We recorded two snakes taking advantage of bee-eater nests in our study area and got evidences of five other vertebrates (three rodents, one bat and one amphibian) using this type of habitat (Table 1).

Sampling of active bee-eater nests resulted in detection of larvae of Tenebrionidae and Lepidopterae and several parasitic mites (e.g. tropical fowl mite *Ornithonyssus bursa*, chicken mite *Dermanyssus gallinae*) and diptera (*Carnus hemapterus*). Adults of nine darkling beetle species (Fam. Tenebrionidae) were observed in high densities around the cliff and entering active and old bee-eater nests (Appendix A).

Sampling of old, inactive bee-eater nests with chromatic traps evidenced the occurrence of many diptera in the nests. The most common ones belonged to the families Psychodidae (detected in 84.8% of the nests, $n = 33$), Phoridae (75.8%), and

Table 1
Vertebrates recorded using old bee-eater nests

Species	Use	References
Rock sparrow <i>Petronia petronia</i>	Breeding	Present study, Oliosio (1974)
House sparrow <i>Passer domesticus</i>	Breeding	Present study
Spanish sparrow <i>Passer hispaniolensis</i>	Breeding	Present study
Tree sparrow <i>Passer montanus</i>	Breeding	Mocci de Martis and Tassara (1994)
Sand martin <i>Riparia riparia</i>	Breeding	Mocci de Martis and Tassara (1994)
Little owl <i>Athene noctua</i>	Breeding	Present study
European roller <i>Coracias garrulus</i>	Breeding	Present study, Meschini and Frascetti (1988)
Pied wagtail <i>Motacilla alba</i>	Breeding	Darolová (pers. comm.)
European starling <i>Sturnus vulgaris</i>	Breeding	Darolová (pers. comm.)
Hoopoe <i>Upupa epops</i>	Breeding	Present study, Martín-Vivaldi (pers. comm.)
African pied starling <i>Spreo bicolor</i>	Breeding	Török (1999)
African Hoopoe <i>Upupa africana</i>	Breeding	Török (1999)
Montpellier snake <i>Malpolon monspessulanum</i>	Shelter,	Present study
	Breeding	Alvarez (1974)
Horseshoe whipsnake <i>Coluber hippocrepis</i>	Shelter	Present study
<i>Apodemus sp.</i>	Breeding	Darolová (pers. comm.)
<i>Muscardinus avellanarius</i>	Shelter	Křištofik (pers. comm.)
<i>Clethrionomys glareolus</i>	Shelter	Křištofik (pers. comm.)
<i>Plecotus auritus</i>	Roosting	Darolová (pers. comm.)
<i>Bufo viridis</i>	Roosting	Darolová (pers. comm.)

Sciaridae (63.6%) but other families were also well represented (Dolichopodidae 21.2%, Ceratopogonidae 21.2%, Cecidomyiidae 15.1%, Milichiidae 12.1%, Carnidae 6.1%, Muscidae 3.0%, Chlorophidae 3.0%, Syrphyidae 3.0%) (Appendix A).

4. Discussion

Our results suggest that the bee-eater acts as an allogenic ecosystem engineer (Jones et al., 1994), in that its activity modifies resources that other organisms can then use. Moreover, it has a significant influence on the ecosystem it occupies since it takes part in basic ecological processes like erosion.

4.1. Bee-eaters as erosive agents

Soil movement can be an important way of redistributing resources in arid areas (e.g. Fossati et al., 1999). However, conservation of soil in arid and semi-arid regions highly vulnerable to erosion (e.g. the Mediterranean basin) is a priority

(Lopez-Bermudez and Romero-Diaz, 1989). Amongst the factors influencing erosion, the role of organisms removing the top soil layer and making it more sensitive to climatic factors has been considered in detail (Ellison, 1946; Black and Montgomery, 1991; Martinez-Rica et al., 1991; Dickman, 1999; Reichman and Seabloom, 2002) and their impact has been proved to be remarkable (Black and Montgomery, 1991; Martinez-Rica et al., 1991). The European bee-eater is one of the few bird species with potential bioturbation activity while digging its nest. We calculated a conservative figure of ca. 13 kg of soil excavated by a pair of bee-eaters during a breeding season. Comparing the importance of different species as bioturbators is difficult because of differences in methods used to estimate removed soil (area and time span considered) and characteristics of each species. Nonetheless, such comparison can highlight the importance of this bird species as an erosive agent. Martinez-Rica et al. (1991) calculated the amount of removed soil by voles (*Pitymys* spp. and *Microtus arvalis*) in the Pyrenees and concluded that bioturbation by Pyrenean voles was a major geomorphologic factor. Extrapolating the amount of soil accumulated in a vole's earthmound to 3 months (the maximum activity period) would render a mean volume of ca. 7.61 and ca. 4.56 kg (data from Martinez-Rica et al., 1991). This suggests that bee-eaters are important bioturbator organisms. Moreover, the soil excavated by bee-eaters is certainly lost since this bird species usually nests in vertical cliffs and thus removed soil falls on the wadi where it will be removed by temporal watercourses.

Bee-eaters were also very likely partially responsible of collapse of parts of the cliffs where they bred. Bee-eaters select those areas of the cliff where soil is thinner and softer (Heneberg and Šimeček, 2004), so that such strata (the easier to dislodge) have many holes. Thus, bee-eater's digging activity decreases the structural integrity of the cliff, facilitating lines of fracture and increasing the likelihood that the cliff will break following such lines. In fact, collapsed pieces usually had on their fracture side remains of bee-eater tunnels. Moreover, we did not detect collapses in a 170 m long neighbouring cliff (probably with a similar edaphic composition as the one here considered since both are the same bank split by a small wadi) where the occurrence of high vegetation on the bed of the wadi precluded bee-eaters from nesting. Therefore, bee-eaters' mining activity increases their importance as habitat modifiers both by removing soil and by providing an ideal setting for abiotic erosive agents.

Our estimation of the amount of soil removed by bee-eaters corresponds to a specific point with a high density of birds. Bee-eaters are usually colonial breeders and can form aggregations of hundreds of individuals (Kossenko and Fry, 1998). Extrapolation of figures obtained in breeding colonies to larger areas would make no sense but it is clear that the impact of bee-eaters in specific places can be considerable. The role of bee-eaters as bioturbators in arid lands can be more valuable given the absence of other organisms with potential bioturbation activity. In semi-arid zones of Europe rodents are reported to be nearly absent (Sánchez-Piñero and Gómez, 1995) and mammals are not very abundant. Thus, bee-eaters may become the major bioturbating organism in these areas.

4.2. Bee-eaters as habitat suppliers

Bee-eaters create habitats that can be used by a remarkable number of organisms for nesting, roosting or completing some stages of their life cycle. Overall, we have compiled information on about 19 vertebrates using old bee-eater nests (Table 1) and many other vertebrates not registered to date probably benefit from cavities excavated by the bee-eater. Darkling beetles, detritivorous species typical of hot-dry ecosystems, also made frequent use of bee-eater nests. Some of the species found in our study area (*Scaurus* spp., *Akis discoidea* and *Elenophorus collaris*) are known to oviposit in cavities (Sánchez-Piñero, pers. comm.) and some *Scaurus* larvae were specifically identified from the ones collected in bee-eater nests. Although other species recorded (*Pimelia*, *Erodius* and *Zophosis*) are more typical of open lands and their larvae are not associated with cavities, adults could visit the nests looking for food. We also recorded the use of old bee-eater holes by a variety of dipteran families (most of them saprophagous but also entomophagous, phytophagous...), whose larvae find food and a suitable place to complete their life cycle (Appendix A).

The use of bee-eater nests by a variety of vertebrates and invertebrates in other non-arid areas has also been recorded. Krištofik et al. (1996) found a remarkable variety of invertebrates in bee-eater nests (see also Petrescu and Adam, 2001). *Phlebotomus major* and *P. perfiliewi*, vectors of *Leishmania* spp., have been found resting in bee-eater burrow-nests (Anonymous, 1993). Similarly, reuse of other bee-eater species' nests by other organisms also occurs. Crick (pers. comm) found ants, termites, toads, rodents and lizards (*Agama agama*) in Red-throated bee-eater' nests (*Merops bullocki*) in Nigeria and Burt (pers. comm.) reported the use of vacant nests of Blue-tailed bee-eaters (*Merops philippinus*) by the snakes *Ptyas mucosus* and *Xenochropis piscator* in Taiwan.

However, the occurrence of this 'new' habitat type in arid lands can be more significant than in other non-arid ecosystems, as resources (including adequate environment, food and shelter) can be scarcer in the former. The chief factors controlling the abundance of invertebrates in arid areas are temperature range, presence of live and dead organic matter, and the availability of water (Noy-Meir, 1985). The widespread use of bee-eater nests by invertebrates is thus not rare as they provide: (i) a mild and humid microclimate (Ar and Piontkewitz, 1992), acting in fact as thermal havens (Seely and Mitchell, 1987; Parmenter et al., 1989), (ii) abundant food (a successful nest has a layer of up to 2–3 cm of detritus and insect remains; Cramp, 1985), that is important in temperate arid zones, where low levels of nutrients (principally nitrogen) impose a major constraint on productivity (West and Skujins, 1978), and (iii) appropriate shelter perfect for the development of many larvae of insects.

One main question when evaluating the potential keystone effect of the bee-eater is whether the resource it provides (i.e. habitat) has population level effects on any of the species using them. Whereas many of the records of animals using bee-eater burrows are primarily opportunistic, at least one species seemed to be more abundant in the presence of the burrows than it would

be in their absence. The rock sparrow is mainly a solitary breeder and colonies reported in the literature are small (up to 30 pairs maximum) and loose (Cramp and Perrins, 1994). In contrast, ca. 100 pairs bred in old bee-eater nests in our study site in at least 2 successive years (Valera et al., 2003). This is, to our knowledge, the largest colony reported in the literature for this species. Abandonment of the cliff by bee-eaters in subsequent years resulted in the disappearance of the rock sparrows and in a usual low breeding density in the study area (pers. obs.). We suspect that some invertebrates, like darkling beetles, may have experienced a similar phenomenon.

4.3. *Bee-eaters favouring ecological webs*

Obviously, the many species dwelling in bee-eater nests increases interspecific interactions that make the whole ecosystem more complex. For instance, Valera et al. (2003) found ectoparasite exchange between bee-eaters and rock sparrows as a consequence of nest reuse by the latter and suggested that such exchange could result in a process of apparent competition. Such interactions may result in a more complex food web. In our study area bee-eaters create nesting places for rock sparrows and offer food and shelter opportunities for darkling beetles that are in turn preyed on by rock sparrows. Given that interspecific interactions are an important force structuring the community, especially in arid ecosystems (Polis, 1991), bee-eaters can play an important role as promoters of ecological webs in such habitat types.

In summary, our results suggest that the European bee-eater acts as an ecosystem engineer influencing abiotic processes and biotic functions. Whereas bee-eater's activity can be important all over its range, its significance may be exacerbated in arid environments where minor perturbations may have wide consequences and where basic resources are scarce. Organisms whose activity substantially alters the physical structure of the environment, influencing both available habitat for other species and various ecosystem processes can become keystone species for a given ecosystem (e.g. Aubry and Raley, 2002). However, Jones et al. (1997) warned that engineers and keystone species are not synonymous. The relevance of the bee-eater as a keystone habitat modifier in arid ecosystems remains to be evaluated.

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Appendix A. Invertebrates recorded in active and old bee-eater nests in our study areas

Order Coleoptera

Fam. Tenebrionidae

Pimelia rotundata

Pimelia variolosa

Pimelia baetica

Pimelia sps.

Scaurus punctatus

Erodius parvus

Scaurus rugulosus

Akis discoidea

Elenophorus collaris

Fam. Chrysomelidae

Galeruca sp.

Order Diptera

Fam. Phoridae

Subfam. Phlebotominae

Fam. Sciaridae

Fam. Dolichopodidae

Fam. Ceratopogonidae

Fam. Cecidomyiidae

Fam. Milichiidae

Fam. Psychodidae

Fam. Carnidae

Fam. Muscidae

Fam. Chlorophidae

Fam. Syrphidae

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