EFFECTS OF SUBSTRATE ON THE DISTRIBUTION OF MAGELLANIC PENGUIN (*SPHENISCUS MAGELLANICUS*) BURROWS

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Abstract.—Slope and texture of substrate influenced distribution of penguin burrows at a large colony of Magellanic Penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. Burrows were most numerous in substrate that consisted mostly of fine particles (silt and clay), with small amounts of sand or gravel. Few burrows were found in substrate with large proportions of sand or gravel. Burrows were more common on slopes than on level ground. More chicks were fledged from burrows in substrates with high amounts of silt and clay and low amounts of sand than from burrows in other substrates. These patterns reflect differences in burrow stability, susceptibility to flooding, and excavation effort. Slope, depth, and texture of substrate should be considered in decisions about protection of penguin breeding habitat.

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Many organisms avoid the effects of environmental extremes by occupying sheltered sites they find or construct. In some cases, the protected sites are necessary for individual survival; in other cases they are necessary for successful reproduction. The importance of these sites to local distribution, abundance, and reproductive success of some organisms has been demonstrated by the introduction of artificial nesting or refuge sites for birds (Enemar et al. 1972, McComb and Noble 1981, van Balen et al. 1982, Hamerstrom et al. 1973), snails (Emson and Faller-Fritsch 1976), and fish and marine invertebrates (Stone 1982, Laufle and Pauley 1985, Solonsky 1985, Walsh 1985).

Terrain and substrate influence the location of refuges constructed by some burrowing species. Prairie dog (*Cynomys ludovicianus*) colonies are generally located on gentle slopes with deep productive soils and few stones, in areas not often flooded (Dalsted et al. 1981). Common mole-rats (*Cryptomys hottentotus*) construct tunnels where soil is moist and easily dug (Genelly 1965), and East-African mole rats (*Tachyoryctes splendens*) preferentially excavate their tunnels into a slope (Hickman 1983). Ants (*Atta sexdens rubropilosa*) make longer tunnels when soil is less dense (Stein and Xavier 1984), and the length and frequency of junctions of rabbit (*Oryctolagus cuniculus*) tunnels depend on soil and site characteristics (Kolb 1985).

Spheniscus penguins are tropical and temperate ground-nesting species that typically nest in sheltered sites. Like other penguins, *Spheniscus* penguins are well equipped to survive in cold water, but they can become heat-stressed when exposed to direct sun and high temperatures on land (Stonehouse 1967, Boersma 1975). Adults can avoid overheating by entering the water or standing in a windy spot. During incubation and chick brooding, however, adults must remain at their nest sites. Temporary absence to avoid heat may cause loss of their eggs or chicks to predators or to temperature stress (unpubl. data). To avoid heat stress for themselves as well as their chicks, breeding *Spheniscus* penguins use nest sites where they can avoid direct insolation (Boersma 1975, Frost et al. 1976, LaCock 1988). These sheltered sites also protect against numerous predators of eggs and chicks. When suitable places under bushes or in natural crevices are not available, these penguins dig burrows.

Burrow construction requires substantial excavation, and substrate stability and permeability will affect burrow quality. Therefore, substrate characteristics should influence burrow abundance. Capurro et al. (1988) suggested that topography and soil were determinants of the location and type of nests constructed by Magellanic Penguins (*S. magellanicus*) at Cabo Dos Bahias, Argentina. Boswall and MacIver (1975) suggested that slope influenced burrow location and that penguins avoided burrowing on flat ground. Blackfooted Penguins (*S. demersus*) constructed fewer burrows at sandy sites (LaCock 1988). We investigated the effects of slope and soil texture on the location, abundance, and reproductive success of burrow nests of Magellanic Penguins breeding at Punta Tombo, Argentina, site of the largest mainland colony of this species.

The breeding season for penguins at Punta Tombo begins when adults arrive at the colony in early September, and lasts through February when most chicks fledge (see Boersma et al. 1990 for a summary). Chicks are present from mid-November through February (a few remain until early March), the warmest part of the year, when temperatures often exceed 30°C. Temperature extremes, along with substantial predation on eggs and chicks, make nest site a critical component of reproductive success.

We expected slope to influence burrow location because inclines facilitate tunneling, and burrows on slopes are less prone to collapse and flooding than those in flat areas. Soil depth should also affect burrow location. In shallow soils sufficient material may not exist to adequately cover the nest chamber. We further expected soil texture to influence burrow construction; the range of available textures presents penguins with a trade-off between ease of moving substrate and burrow stability. Soil with large amounts of small gravel and sand is easy to move but is noncohesive and unstable. Soil composed entirely of smaller particles (silt and clay) is more cohesive but difficult to penetrate. Therefore, substrate containing intermediate amounts of sand, silt, and clay should be more favorable for burrow construction than soils of one particle size. Large particles (rock and large gravel) are both difficult to excavate and noncohesive, and should be unfavorable in any amount.

Slope and substrate characteristics at any location in the colony can influence both the ability of penguins to construct burrows, and the quality of the location as a burrow nest site. We therefore expected the effects of these characteristics to be reflected in patterns of burrow density as well as in patterns of reproductive success. Adults with burrows in substrates more prone to flooding or collapse should fledge fewer chicks per nest than those with burrows in less flood-prone and more cohesive material.

Understanding the importance of physical features in the nesting ecology of penguins has conservation and management value. Colony location, burrow density, and nesting success may in some cases be constrained by physical features. As coastal habitat is increasingly altered by humans, protecting areas that have desirable qualities for nesting is important in maintaining populations of burrowing seabirds. In addition, modifying physical features to improve habitat quality is a management tool that may be useful in maximizing populations of penguins and other burrowing species in protected areas.

METHODS

We studied a large colony of Magellanic Penguins at Punta Tombo, Argentina (44°02′S, 65°11′W) (see Boersma et al. 1990). In early February in 1987, 1988, and 1989, and early October in 1987 and 1988, we surveyed the colony along north-south and east-west transects. In 100 m^2 plots located at regular transect intervals of 33.3 m across most of the colony, we counted all penguin nests in each plot, classified all nests by type (see below), determined the number of chicks present in each type of nest (February surveys only), estimated the percentage of plot area covered by vegetation (bushes or grasses), and evaluated the substrate texture. In February 1989 we measured the slope at each plot sampled with a hand-held clinometer.

We classified substrate as *rock* (exposed bedrock), *shell* (shell fragments could be visually identified), *gravel and loose rock* (particles larger than 2 mm in diameter and smaller than 10 cm, except for a few cases with loose flat rocks of up to 30 cm maximum length), *sand* (particles that, when dropped from about 15 cm, fell to the ground and were roughly 2–0.5 mm), and finer particles that felt smooth to the touch (silt and clay). Although gravel and loose rock included some large material, the vast majority of particles in this category were small rounded pebbles, and we refer to material in this category as gravel. The particle-size categories do not precisely correspond to those of the standard U.S. Department of Agriculture soil classification system. The main difference is that our silt and clay category includes the fine sand of the standard system.

We estimated the approximate percentage by volume of each substrate component in the surface layer (top 5 cm) of each sample plot. Estimates were standardized by independently categorizing several sample plots until agreement among all observers was reached. At each sample plot, the two members of the survey group reached agreement on the substrate composition. These estimates are rough, but adequate for comparison. For analysis, the percentage estimates of each substrate component were lumped into the following groups: 0–10%, 11–20%, 21–40%, 41–60%, 61–80%, 81–90%, and 91–100%. We think these groupings conservatively reflect the discrimination power of the estimation technique. For 25 sample plots where substrate texture was estimated in each of the 5 surveys, the mean standard error was 10% for gravel, 8%

for sand, and 9% for silt and clay. For components that constituted >80% or <20% of the sample, errors were much lower.

We coded all nest sites in each plot according to type: *burrow* (a nest with a roof made of soil or gravel), *bush* (a nest with a cover of vegetation), or *scrape* (a saucer-like depression in the soil, without a roof or covering bush). We used only active nests in our analysis. A nest was considered active if an egg, chick, or adult penguin was in the nest, or if fresh guano, green nesting material, or freshly dug soil was present. We excluded bush nests from our analysis because we expected substrate characteristics to affect bush nests less directly than burrow nests. We included only those sample plots where bushes covered 10% or less of the plot so that burrow density and numbers of chicks present would not be confounded by large numbers of bush nests. There were 1,097 sample plots that met this restriction (about 36% of the surveyed area).

We excluded the relatively small number of scrape nests from the analysis except in examining fledging success patterns. Active scrapes were lumped with burrows in this case because of the difficulty of determining in February whether a scrape began the season as a burrow and had subsequently collapsed to form a scrape. Because birds using scrapes have lower fledging success than those using burrows (unpubl. data), the inclusion of scrapes with burrows caused fledging success at burrows to be slightly underestimated.

To examine the effects of substrate on reproductive success, we estimated the mean number of chicks fledged per burrow in each sample plot by dividing the number of chicks (except those in bush nests) present in early February by the number of active burrows and scrapes in the the plot. The small number of chicks present in early February that did not eventually fledge partly offsets the number of chicks that fledged earlier in the season and were not counted. (Each breeding season, fledging began in mid-January, peaked in mid-February, and continued until late February; a small number of chicks did not fledge until early March.) Regardless of its absolute accuracy, this estimate of fledging success is adequate for comparative purposes. The percentage estimates of each substrate component in the samples were lumped into groups of 0–10%, 11–30%, 31–60%, and 61–100%. The use of broader categories than those used in burrow-density analysis was necessary to achieve sufficient sample sizes in each category. To avoid the confounding effects of density on reproductive success, we analyzed low-density (0–10 nests per 100 m^2) and high-density (>10 nests per 100 m^2) samples separately.

In December 1985 and January 1986 we took a soil sample in each of twenty 100-m^2 plots where burrows were the predominant nest type. Sample sites were at roughly similar distances from the beach (200–400 m) to control for differences in habitat quality due to proximity to the ocean. Vegetation in the 100-m^2 soil sample plots was sparse, and ranged from areas that were bare to areas that had grass or herb cover or a few bushes (bushes covering up to 10% of the sample plot). We judged the general slope of each soil sample area as either flat (0–4% incline) or sloped (≥5% incline). In each soil sample plot we measured the entrance height and length of up to 10 burrows to the nearest centimeter with a meter stick. At the center of each plot, we sampled soil at 2 or 3 depths: a top sample 10 cm below the surface, a middle sample when there was a change in texture or color in the soil profile, and a bottom sample either at a depth below the deepest nests or when we couldn't dig any deeper with a shovel. Two samples did not have sufficient material in the top subsample for analysis of sand, silt, and clay, and they were excluded.

We sifted substrate through screens to determine soil texture in the 20 soil samples (Bouyoucos 1927). Substrate particle-size intervals were defined by the U.S. Department of Agriculture system: gravel = 2 mm or more, sand = 2 mm to 50 mu, silt = 50 mu to 2 mu, and clay = less than 2 mu. This scale agrees roughly with the scale we used in the survey samples, except that material classified as fine sand in this system was largely included with silt and clay in the survey data. We determined the percent-by-weight of gravel in the soil and analyzed a subsample of 50 g of the remaining nongravel material to determine the amounts by weight of sand, silt, and clay. We measured calcium carbonate content gravimetrically (U.S. Salinity Laboratory Staff 1954). Between-method comparison of substrate composition is valid only at a general level due to the discrepancies between particle-size classes, the use of percent-by-volume in the survey data set and percent-by-weight in the soil samples, and the concentration of soil sample plots close to the sea.

In February 1989, we measured the length, width, and height of 15 burrows and 5 scrapes. In addition, we measured roof thicknesses and depths of 75 burrows with partially collapsed roofs ("skylighted" burrows) to determine minimum roof thickness of burrows.

We determined soil hardness for the various classes of pure substrate textures: silt and clay, wet sand, dry sand, and 2 sizes of gravel. Hardness was expressed in kg and was proportional to the force required to penetrate the substrate to a depth of 12 cm using a push-pull gauge (9 kg maximum, 100 g increments) with a 5-mm cross-section diameter plunger. Substrate hardness was also measured for a wide range of representative substrates in the colony by averaging 5 push-pull gauge measurements made in front of each of 64 burrows in various substrates. These measurements were taken in the disturbed soil at burrow entrances, where hardness was generally within the range of the gauge. Away from burrow entrances,

TABLE 1. Hardness ($\bar{x}$ ± SD) of pure substrate texture classes at Punta Tombo. Hardness (in kg) is proportional to the force required to penetrate substrate to a depth of 12 cm using a push-pull gauge with a 5-mm-diameter plunger (cross-section area = 1.96×10^{-5} m^2). All samples in silt and clay exceeded the 9-kg maximum of the gauge. Average diameter of gravel particles is in parentheses.

Substrate	Hardness	*n*
Silt and clay	>9.0	30
Gravel (1 cm)	5.0 ± 1.2	10
Gravel (3 cm)	4.4 ± 1.4	22
Wet sand	6.4 ± 1.5	11
Dry sand	4.0 ± 1.4	34

most measurements in all soil types exceeded the 9 kg maximum of the gauge. To investigate the effect of soil hardness on burrow stability, we measured the lengths of burrow "trails" (Boswall and MacIver 1975) in soils of different hardness. Burrow trails are the visible traces on the surface of the ground left by receding burrows as they collapse and are reexcavated by penguins.

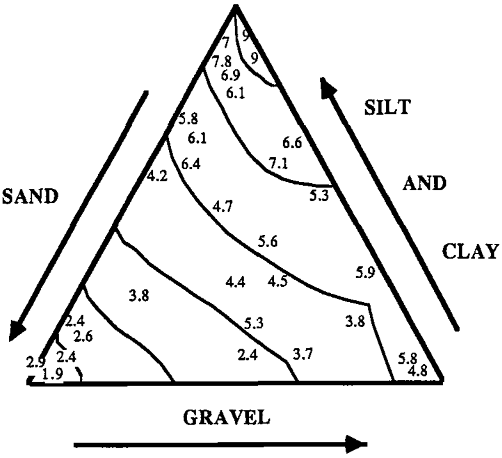

Fig. 1. Distribution of substrate hardness (maximum = 9) in mixed substrates at Punta Tombo in February 1989 based on measurements at 64 locations. Measurements from substrates of the same composition were averaged. Lines connect substrate compositions of approximately equal hardness. Top corner represents substrate of 100% silt and clay, lower left is 100% sand, and lower right is 100% gravel.

RESULTS

Based on all sample plots from the colony-wide surveys (3,031 plots, $n = 19{,}937$ active nests), slightly more breeding pairs used bushes (52%) than burrows (47%). Only a small proportion (1%) used scrapes. Fledging success at burrows was significantly higher than at bushes ($\chi^2 = 15.30$, df = 1, $P < 0.001$). This may reflect factors other than nest quality, however, because burrows tended to be closer to the sea.

Soil samples from a depth of 10 cm contained (by weight) a large amount of gravel (mean [± SD] = 42 ± 21%). The texture of the remainder varied from sand to silty loam. Proportions of nongravel components were as follows: sand 45 ± 21%, silt 9.4 ± 5.3%, and clay 3.6 ± 2.3%. The more approximate survey data also indicate a large fraction (by volume) of gravel (30 ± 29%), but lower amounts of sand (18 ± 27%) and greater amounts of silt and clay (42% ± 31%) because much of the fine sand was included in the silt and clay category. Soil texture for the whole colony was characterized as largely sand and gravel in the standard U.S. Department of Agriculture soil classification system. Areas closer to the ocean have higher proportions of these coarse particles.

Visual inspection of soil profiles at Punta Tombo indicated the soil was relatively undifferentiated, and correlations between proportions of most substrate components in top and middle soil samples were high (sand $r^2 = 0.78$, silt $r^2 = 0.70$, clay $r^2 = 0.62$, calcium carbonate $r^2 = 0.86$). Proportions of gravel were poorly correlated ($r^2 = 0.18$), with more gravel at the surface than at depth. Thus the composition of the top of the soil was similar to that found at greater depth except that there was usually less gravel below 10 cm.

The pure texture classes of substrate differed markedly in hardness, with silt and clay highly resistant to penetration, and dry sand easily penetrated (Table 1). Generally, gravel was of intermediate hardness. A similar pattern was found in representative mixed-texture substrates (Fig. 1). Substrates with high levels of silt and clay were hard; those with large amounts of sand were soft. Substrates with large amounts of gravel were intermediate, and were more variable, due to variability in size and position of particles struck by the gauge.

A typical burrow for a Magellanic Penguin has a relatively wide entrance that narrows to a short neck and then widens slightly into a chamber where the eggs are laid (see Boswall and MacIver 1975). Burrows at Punta Tombo ranged from little more than open scrapes to sizable "tunnels" >1 m in length. In 15 burrows

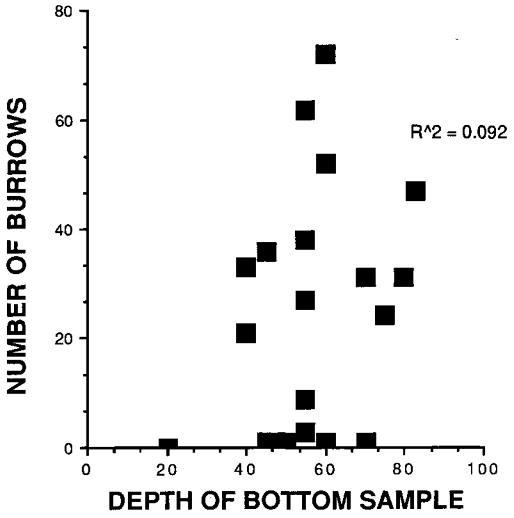

Fig. 2. Number of penguin burrows in the 100-m^2 soil sample plots ($n = 20$) versus depth of the bottom soil sample. This depth is approximately equivalent to the depth of soil at the sample site.

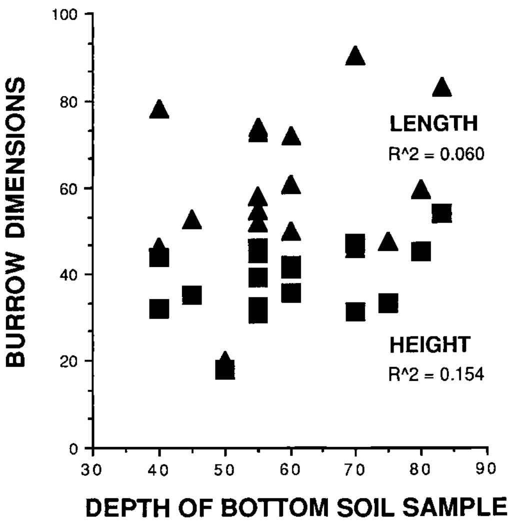

Fig. 3. Burrow length (▲) and height (■) versus depth of bottom soil sample. This depth is approximately equivalent to the depth of soil. Number of sample areas = 20.

where chicks fledged the mean (± SD) length = 59.3 ± 18.7 cm, width at entrance = 56.3 ± 11.4 cm, width at neck = 37.3 ± 5.4 cm, and height = 21.1 ± 3.8 cm). To construct these burrows, penguins had to remove an average of 0.05 ± 0.02 m^3 of substrate. In 5 active scrapes, mean length = 114.4 ± 24.7 cm, width = 80.8 ± 7.0 cm, and maximum depth = 15.0 ± 4.5 cm). An average 0.12 ± 0.03 m^3 of material were excavated to create one of these scrapes, more than was excavated to construct a burrow. The mean depth to the bottom of the nest cup of a burrow was 31.4 ± 7.2 cm ($n = 75$), and the mean roof thickness was 6.8 ± 4.9 cm ($n = 75$). These are minimum values, because they were from burrows with partially collapsed roofs. Roof thickness can be considerably greater in burrows dug into steep slopes.

Soil thickness is an obvious limiting factor in burrow distribution. Penguins cannot dig burrows into rock, and we found no nest sites on exposed rock. Nests of all types were scarce, and burrow nests were generally absent from areas where soil was thin. In the one soil sample plot where soil was 20 cm thick, no burrows were present. All other areas we sampled had soils deeper than 40 cm. Mean depth to the bottom soil sample was 56.7 ± 15.1 cm (range = 20–83 cm, $n = 20$). Among samples with soil at least 40 cm deep, burrow density was not strongly related to soil depth (Fig. 2). Nor were there strong relationships between burrow height or length and soil depth (Fig. 3).

Given the generally deep soils in our sampling areas, we could not determine the extent to which shallow soil influenced burrow density. We used Capurro et al.'s (1988) data from Cabo Dos Bahias to test if nest density was significantly lower in shallow soils. Their data combined both bush and burrow nests. Areas with shallow soils (<15 cm deep) had fewer nest ($\bar{x} = 13$ nests per 100 m^2) than areas with thicker soils (38 nests per 100 m^2) (Mann-Whitney U, $P < 0.001$). The scarcity of nests of all types in the shallow soil areas can probably be attributed to the effective exclusion of burrows from these areas (15 cm is generally too shallow for burrows), and the presence of fewer bushes. We believe that shallow soils, where they occur, have similar effects on nest abundance at Punta Tombo.

Unlike soil depth, slope is variable at Punta Tombo, and was an important determinant of burrow distribution. In the February 1989 survey, among adjacent sloped (≥4% slope) and flat (<4% slope) plots of similar, high-quality substrate (≤20% sand, ≤30% gravel, ≤35% sand and gravel combined, between 60 and 95% silt and clay, and insignificant amounts of rock and shell), mean densities were significantly greater

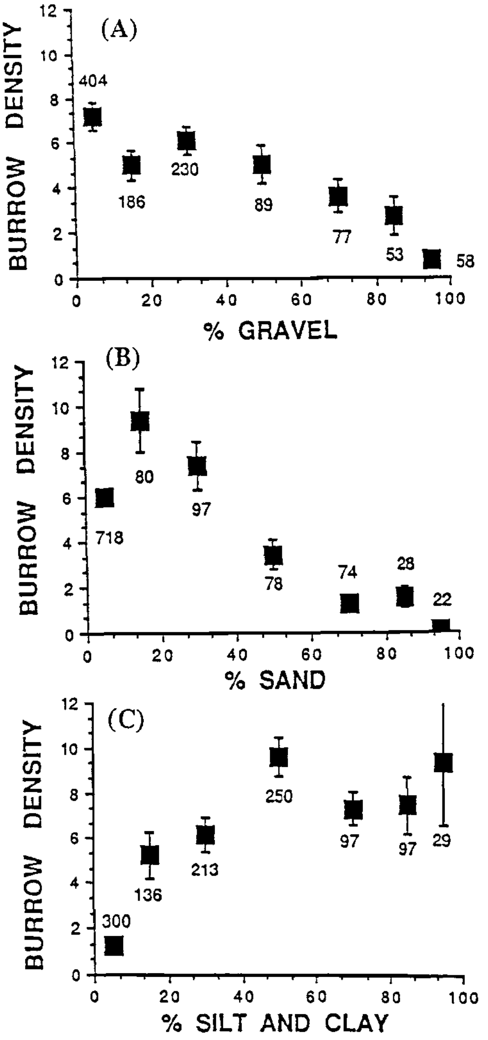

Fig. 4. Burrow density and soil texture. Burrow density (A) by % gravel substrate, (B) by % sand in substrate and (C) by % silt and clay in substrate. Vertical lines indicate ±standard error of the mean. In some cases SE does not extend beyond the plot icon. Total sample size for each figure = 1,097. Sample sizes for each % category are shown.

in the sloped plots (paired *t*-test, $t = 3.83$, $n = 10$, $P < 0.005$). Also, fewer burrows (16 ± 20) were present in flat soil plots than in sloped plots (38 ± 19 burrows; *t*-test, $t = -2.36$, df = 18, $P < 0.05$). This trend is not without exceptions; some of the most densely settled parts of the colony are flat. Even in the flat areas, slope at the micro-site scale favors burrow location. Flat areas did not differ significantly from sloped areas in proportions of major soil texture components (gravel, flat vs. slope, *t*-test, $t = -1.53$, df = 18, $P > 0.10$; sand, $t = 1.72$, df = 17, $P > 0.10$; silt and clay, $t = .96$, df = 17, $P > 0.20$).

We found that burrow density correlated highly with soil texture (Fig. 4). Density was highest in areas of least gravel, decreased slowly as gravel content increased, and declined quickly as gravel exceeded 50%. A high proportion of sand was also unfavorable for burrows, with highest burrow densities in soil of 10–20% sand. Areas with >60% sand had few burrows and those with very high amounts of sand (>90%) had virtually none. This is consistent with observations that in sandy areas burrows collapsed frequently. Penguins often dug burrows after rains when sand was moist, but many of these burrows collapsed when the sand dried out and particle cohesion was reduced. Large numbers of burrows also collapsed during heavy rains when sandy soil became saturated. Areas with low proportions of silt and clay had low burrow density. Burrow density increased rapidly as silt and clay increased until these components formed about 50% of the substrate. At greater than 50% silt and clay, burrow density was high and roughly uniform. The combined effects of these patterns are related (Fig. 5).

Fledging success (Fig. 6) was roughly similar to nest density patterns for sand and silt and clay. Highest fledging success occurred in areas with high amounts of silt and clay and low amounts of sand. Increased amounts of gravel had an increasingly negative effect on burrow density (Fig. 4A), but gravel had an unpredictable effect on fledging success (Fig. 6A), with perhaps a beneficial effect at proportions >60%. Small but significant amounts of sand favored increased burrow density (Fig. 4B), but not fledging success, and may have had a negative effect (Fig. 6B). Low-density samples (0–10 nests per m^2) best reflect the effects of substrate on fledging success, because in high-density samples (included in Fig. 6) substrate effects were more likely to be obscured by biological effects associated with high density. The negative effects of sand on reproductive success were apparent even at high density.

Mean burrow length in the soil sample plots was 62.9 ± 23.0 cm ($n = 130$) and mean entrance height was 39.7 ± 10.9 cm ($n = 130$). The depth and height of the burrows was not significantly related to soil texture (% gravel with burrow

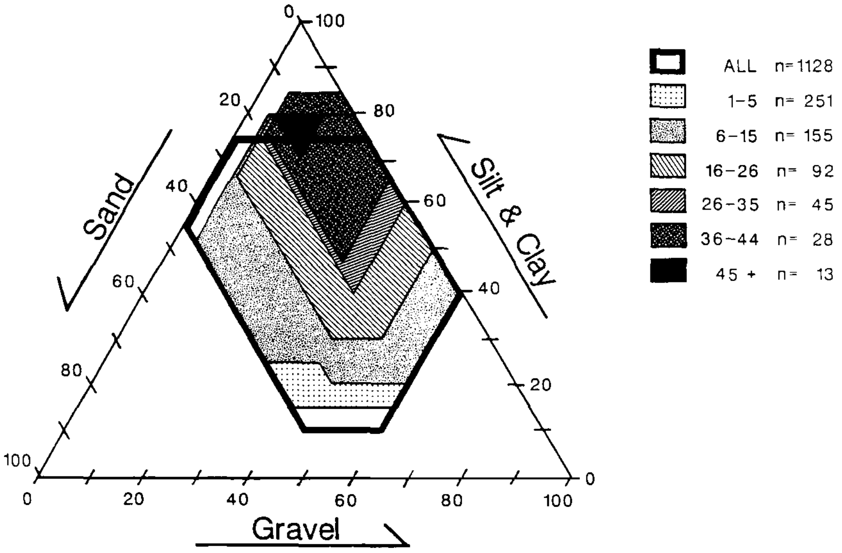

Fig. 5. Actual distribution of burrow density over soil textures at Punta Tombo from 1,128 100-m^2 sample plots. All plots were from areas of the colony with ≤10% bush cover. Lines include ±1 standard deviation of the mean of each texture class for each category of burrow density. Sample size for each category of burrow density is shown. Nearly half of the areas sampled (n = 544) had no burrows.

length, r^2 = 0.03; % gravel with height, r^2 = 0.04; % sand with length, r^2 = 0.02; % sand with height, r^2 = 0.04; % silt and clay with length, r^2 = 0.43; and % silt and clay with height, r^2 = 0.00). Mean lengths and heights of burrows in flat sample areas (mean depth = 56.7, height = 36.2) were slightly smaller than in sloped samples (depth = 63.3, height = 40.5), but the difference was not significant (depth, t-test, t = 0.78, df = 15, $P > 0.20$; height, t = 1.03, df = 15, $P > 0.20$).

Burrow-trail length correlated negatively with substrate hardness (Fig. 7). This is consistent with the observation that burrows collapse frequently in soft sandy substrates, and rarely in harder substrates. The correlation probably underestimates the strength of the actual relationship because we could not control for penguin site tenacity or burrow age, which are expected to strongly affect trail length. Substrate hardness appears to be a good indicator of cohesiveness and susceptibility of burrows to collapse.

Burrow nest sites do not appear to be limited as approximately 10% were not used. The proportion of burrows that were unoccupied (13%, n = 710) in poor substrate (>60% gravel or sand or >80% gravel and sand combined, and ≥20% silt or clay) was greater than in good substrate (≤40% sand and gravel combined, and >40% silt and clay) (9% unoccupied, n = 4,518; χ^2 = 11.60, df = 1, $P < 0.001$).

DISCUSSION

Distribution and density of penguin burrows are influenced by substrate depth, slope, and texture. The limitations imposed by soil depth are obvious. Penguins cannot dig burrows in rock, although they make use of crevices and overhangs. Penguins rarely construct burrows in shallow soil (<15 cm deep). The bottom of the nesting cup in skylighted burrows was ca. 31 cm below ground surface; we suggest that soils must be >30 cm deep to be suitable for burrow construction. Nests of all types may be limited in areas of shallow soils because bushes may be less prevalent and smaller on very shallow soils.

Despite its potential for limiting burrow distribution, soil depth is probably not a widespread limitation at Punta Tombo. Except near a few rock outcrops, soil depth is generally >30 cm. Furthermore, the absence of a significant correlation between soil depth and burrow density at Punta Tombo indicates that soil depth >40 cm has no effect on burrow distribution. Soil depth may be more important at other colonies (Cappuro et al. 1988), where soil is thinner.

Where the soil is deep enough for burrows, slope is an important factor in burrow distribution. To dig a burrow, a penguin anchors itself with its bill and flippers and removes the soil with its feet. Even a slight slope allows the bird to anchor itself and dig more effectively (pers. obs.). When burrows are dug into a slope, excavated material is less likely to slide back into the burrow. Only if a penguin first excavates a sufficient depression (i.e. creates a slope) where it can anchor itself and remove material, can it build a burrow in flat ground. This is equivalent to creating at least a partial scrape before building the actual burrow. Because scrapes require two to three times more excavation than burrows, burrow construction requires substantially more time and effort on flat ground than on a slope.

Burrows in flat areas are also prone to flooding and collapse. On a slope, burrows open relatively horizontally, whereas on flat terrain,the opening faces upward. Because the outer part of the entrance is generally wider than the nest cup, a sky-facing burrow can trap substantial amounts of water during rainstorms. Moreover, some flat sites are in low spots where water collects during heavy rain. These spots can be under up to 0.5 m water. Flooding is a substantial cause of egg and chick mortality in some years. In addition, because of slower drainage of flat areas during and after rainstorms, soils in these areas are more likely to become saturated than similar soils on slopes. In mixed-textured substrates, saturation reduces soil cohesion, which can cause burrows to collapse. In very sandy substrates, moderate amounts of

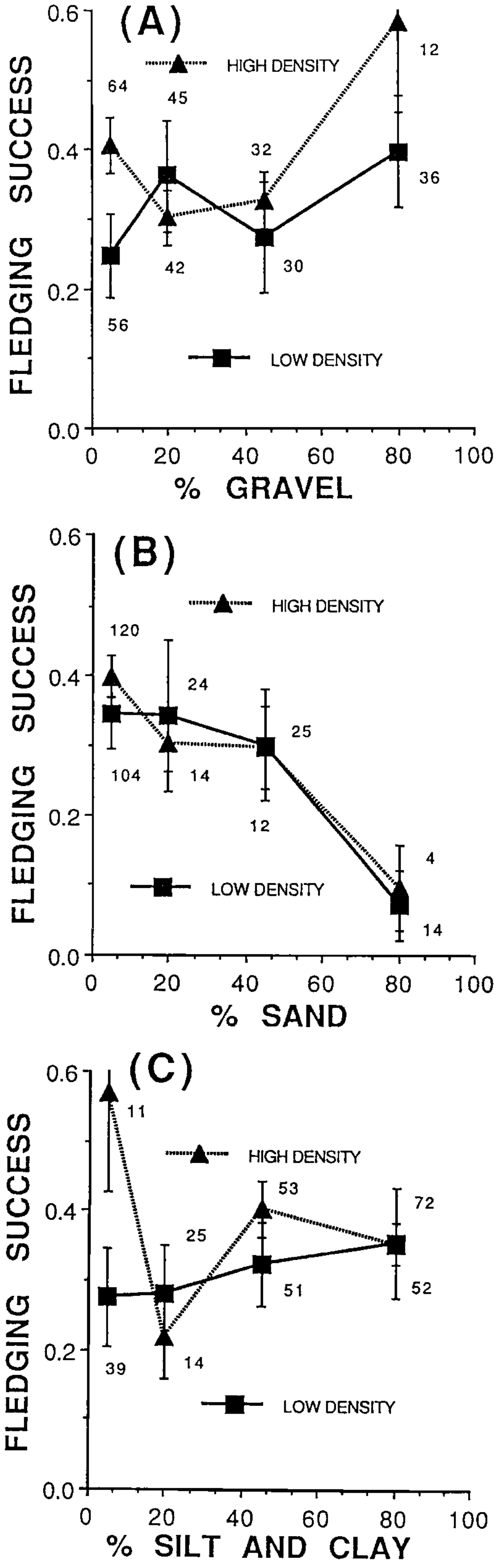

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Fig. 6. Soil texture and fledging success at burrows and scrapes (February samples only) Fledging success (A) by % gravel in substrate, (B) by % sand in substrate and (C) by % silt and clay in substrate. Low density includes all samples with 0–10 nests per 100 m^2. High density includes all samples with >10 nests per 100 m^2. Vertical lines indicate ±standard error of the mean. Fledging success was defined as number of chicks present in burrow and scrape nests in early February in each plot divided by the number of burrow and scrape nests active during the season in that sample. Almost all chicks that were alive in early February eventually fledged. Sample sizes for each category are shown.

moisture increase cohesion (Table 1), but this cohesion is lost quickly as the sand dries. Furthermore, burrows dug into level ground tend to have thinner and therefore more collapse-prone roofs than those in slopes. At the least, burrow collapse increases vulnerability to heat stress and predators, requires reexcavation, or can cause nest desertion. Often the results are more serious, and eggs and chicks are destroyed. Even adults can become trapped and die in their collapsed burrows (pers. obs.). Penguins may select burrow sites on slopes to avoid flooding and burrow collapse.

Slope may influence substrate effects in some situations. For example, soils with high proportions of silt and clay are relatively impermeable. Burrows in a high silt and clay substrate on a flat may fill with water during a heavy rain and remain flooded for several days. Prolonged saturation is likely to lead to burrow collapse. In contrast, burrows in the same substrate on a slope are unlikely to flood or collapse, because water drains without soaking into the substrate.

High proportions of sand and gravel have large negative effects on burrow density (Fig. 5). Silt and clay have a negative effect only at very high amounts (>85%), and even in substrates that are nearly all silt and clay, burrow density is high. The negative effects of gravel are mainly due to difficulty of digging in noncohesive material. As the proportion of gravel increases, the substrate is less easily excavated. Once a burrow is excavated, the amount of gravel has no consistent effect on burrow quality (Fig. 6A). Fledging success patterns suggest that very high proportions of gravel may be favorable for burrow stability, though this is inconclusive. At one regularly observed site with a substrate of mostly gravel, burrows changed little over the course of five seasons, which indicates that the substrate is stable and resistant to collapse. Other locations with high amounts of gravel contain burrows that collapsed frequently. The stability of gravel as a burrow substrate is probably dependent on particle size. The variability in particle size of gravel at Punta Tombo, along with differences in the fractions of finer particles in the substrate, probably accounts for the lack of a consistent relationship between fledging success and proportion of gravel. This relationship may also be obscured by sample location effects. Most of the samples with very high proportions of gravel are close to the sea, and therefore may provide higher-quality habitats for reasons unrelated to substrate.

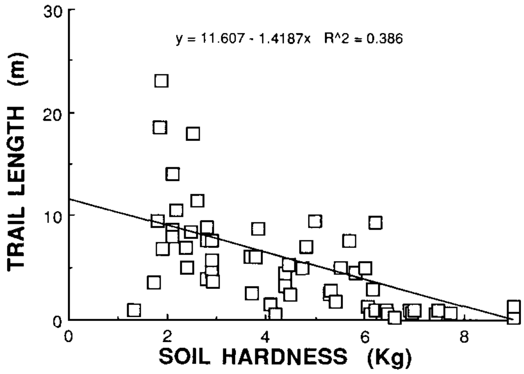

Fig. 7. Length of burrow trails by soil hardness. Hardness is expressed in kg and is proportional to the force required to penetrate substrate to a depth of 12 cm with a push-pull gauge with a 5 mm diameter plunger. Longer burrow trails indicate more frequent burrow collapse due to less cohesive, often sandier, substrate ($n = 61$).

Sandy soil is soft and easily moved, but may be so noncohesive that excavation of a burrow is impossible except where roots of grass or bushes hold the roof together. Even where sand is present in moderate amounts, substrates are noncohesive (Fig. 1). Once constructed, burrows in sandy soil often collapse (Fig. 7), particularly when the soil dries or is exposed to heavy rain. The semiarid climate of Punta Tombo, characterized by long dry periods punctuated by infrequent but sometimes heavy rain, makes sand a poor substrate for burrows.

Though large amounts of sand are associated with lower burrow density and fledging success, small but significant amounts of sand (10–20%) have a positive effect on burrow density (Fig. 4B). Where the other major soil components are silt and clay, a small measure of sand makes the ground less difficult to penetrate and excavate. Substrates dominated by silt and clay are extremely hard when dry (Fig. 1). With a small amount of sand, a silt and clay substrate is softer, but still sufficiently cohesive for stable burrows. Silt and clay have negative effects on density only at very high proportions when the soil is extremely hard. Once constructed in a cohesive silt and clay substrate, a burrow is very sturdy and resistant to collapse (Fig. 6C, low-density line). In addition to being highly cohesive, silt and clay soil becomes saturated less rapidly than coarser substrates, so burrows are less prone to collapse during rainstorms.

Substrate effects on fledging success are more consistent and are in better agreement with predictions in samples with low burrow density than in samples with high density (Fig. 6). For instance, as amounts of silt and clay increase, burrows are expected to be more resistant to collapse and therefore birds nesting in them are more likely to fledge chicks. The expected trend is present at low, but not at high, density (Fig. 6C). This is probably due to intraspecific interactions and predation in high-density areas, which overshadow substrate effects. The negative effects of increased sand are apparent even at high density (Fig. 6B), which indicates that not all substrate effects are obscured by biological factors at high density.

We could not assess accurately the relative importance of excavation costs and reproductive success effects (e.g. chance of flooding or burrow collapse) of different substrates on burrow distribution. Burrow length and height in different substrates are similar. This indicates that once a burrow is started, soil texture does not affect digging ability enough to modify burrow length or height. Burrows must be long enough to protect the adults, eggs, and chicks from extremes in temperature, and must not be accessible to predators nor so large as to make collapse likely. These requirements may be so stringent that burrows in more difficult terrain are constructed to the usual size regardless of cost. Densities may reflect those excavation cost differences. On the other hand, the invariant dimensions of burrows may indicate that less densely settled substrates are not necessarily significantly more costly to excavate. Thus, lower densities in these areas may reflect penguins' recognition of the poor reproductive potential of nesting there. This interpretation may also be inferred from the higher burrow vacancy rate in areas with poorer substrates. Presumably penguins do not select these poorer sites even when empty burrows are available and digging costs are minimal.

Distinguishing between these mechanisms is not possible at present, and it may be that both are important. For example, the burrow-density patterns with respect to sand and gravel seem to reflect excavation difficulty, with density highest in substrates with small but significant amounts of sand and minimal amounts of gravel. These substrates are the least difficult to excavate, but they are not characterized by the highest fledging success. At the same time, burrow densities are also highest in substrates with the most silt and clay, where fledging success is greatest, but excavation costs may be relatively high.

Distribution, density, and quality (measured by fledging success) of penguin burrows at Punta Tombo are strongly affected by terrain and substrate. We found that the most favorable substrate for Magellanic Penguin burrows is soil >30 cm deep, at least slightly sloped, and with an intermediate texture dominated by fine particles. In choosing coastal habitats for protection of *Spheniscus* penguins, locations with these substrate characteristics should be preferred. These characteristics also should be considered in attempts to improve penguin nesting habitat damaged by human activities.

Substrate improvement to increase breeding success of penguins and other burrow-nesters may be an important conservation approach in damaged habitats. Solutions could include maintaining adequate burrow substrate, modifying slope, or providing artificial nests or favorable burrowing substrate. For example, guano harvesting along the Peruvian coast removes nesting substrate down to bare rock. One possible conservation measure would be to leave areas of unharvested substrate at least 40 cm thick on portions of the islands for nesting Humboldt Penguins (*S. humbolti*) and diving petrels. The provision of additional suitable substrate for burrow nesters could further increase the number of birds able to construct nests at a site, and reduce losses of eggs and chicks (and even adults in some cases) due to temperatures stress, predation, flooding, or nest collapse. As modification of coastal areas by humans increases, knowledge of how to protect habitat and improve damaged habitat will become more important.

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