have found that thresholds for perceiving very low spatial frequency depth corrugations (< 0.1 cycle/degree) are substantially higher when the depth contours generate expansion transformations than when they generate shear transformations. This was true for both stereoscopic and parallax depth corrugations.

Taken together, these results suggest that the falloff in low spatial frequency sensitivity is greater when the surfaces generate expansion-compression rather than shear transformations. Alternatively, the overall shape of the sensitivity functions may be similar, but the curves may be displaced relatively along the spatial frequency axis. The latter hypothesis would predict that the sensitivity for high spatial frequency depth corrugations should be greater for surfaces that produce expansion transformations. Such an anisotropy was recently reported for the simpler task of detecting patterns of relative motion (*9*). Our own studies of sensitivity to depth corrugations show a slight tendency in this direction, together with a small shift in the region of peak sensitivity toward a higher spatial frequency for surfaces that generate an expansion transformation. This would be expected if the spatial extent of local processing is less in a direction parallel to the direction of disparity or parallax motion.

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Territorial Bell Miners and Other Birds Affecting Populations of Insect Prey

Abstract. *Bell miners (*Manorina melanophrys*) feed primarily on the lerps and nymphs of psyllids, and they defend communal territories against other bird species. As bell miners were removed experimentally from a psyllid-infested patch of eucalypt forest, birds of 11 other species moved in to feed on psyllids and within 4 months they eradicated the infestation. This shows the ability of other birds to control these insects in the absence of bell miners and the value of interspecific territoriality to bell miners.*

Bell miners (*Manorina melanophrys*) are aggressive honeyeaters (Meliphagidae) from southeastern Australia. They defend communal territories in the eucalypt forest canopy against other birds (*1*), including much bigger species. Up to 90 percent of the bell miners' diet consists of nymphs, sweet secretions, and lerps (protective carbohydrate covers) of psyllids (Homoptera: Psyllidae) (*2–4*), but wherever bell miners occur trees appear unhealthy, and foliage remains infested with these insects. Trees recover only if bell miners depart, and it was assumed that both events follow an initial decline in psyllids. However, when a landowner removed bell miners he observed that other birds invaded and controlled the psyllids, and the trees then recovered (*5*).

We repeated the experiment by removing all 34 bell miners from a small colony in Olinda State Forest between 22 July and 5 August 1981. The site of about 3 ha is at an altitude of 250 m, at 37° 50′S, 145° 22′E (near Melbourne), with annual rainfall of 1200 mm. Trees were mainly *Eucalyptus obliqua* and *E. cypellocarpa*, reaching heights of 30 m and showing severe defoliation and dieback due to endemic psyllids (*Glycaspis* spp). The birds were caught in barely visible stationary mist-nets; they were banded and released in psyllid-infested forest 45 km southeast, where there was already a larger colony of bell miners. They did not return to Olinda.

Bird populations were measured at intervals before and after removal by standard 20-minute searches in which all birds observed on the 3 ha were counted. Psyllid populations were estimated mainly by counting lerps on fallen leaves and litter that were collected monthly from 24 trays (0.2 m^2) under selected trees. Similar measurements of birds and psyllids were made in comparable study sites in adjacent healthy forest and in a psyllid-infested forest nearby.

The experimental site was not reinvaded by bell miners (Fig. 1), although another colony remained only 300 m away. Instead, small flocks of nomadic insectivorous birds invaded and began eating psyllids at a greater rate than had been achieved by the bell miners. A few bark-gleaning species also appeared. Numbers of birds remained high in August and September and suddenly declined in October. A smaller temporary influx occurred in early November, possibly corresponding with another generation of psyllids, but thereafter numbers were low and similar to those on the healthy control nearby. Numbers of birds on the two control areas showed much smaller seasonal changes.

Numbers of psyllids at the experimental site dropped rapidly when bell miners were removed and remained close to zero thereafter (Fig. 1). Few psyllids occurred on the healthy control at any time. Numbers in the psyllid-infested control fluctuated, but the dramatic disappearance on the experimental site was not paralleled there or at any of several other sites monitored. Subsequent improvement in tree health was revealed by a 15 percent increase in epicormic foliage observed on the experimental site 6 months after bell miners were removed, compared with a 4 percent increase on the healthy control and no net change on the psyllid-infested control.

Before removal bell miners constituted 64 percent of birds observed on standard searches; most others were understory species. The bell miners spent about 36 percent of the daylight hours foraging, and each consumed psyllids or lerps at an overall mean rate of 12 per minute (30 observations, each of about 1 minute). The mean weight of a bell miner was 30 g. After removal of bell miners, the most common psyllid-eating birds were striated thornbills, *Acanthiza lineata* (mean weight, 7 g; 24 percent of birds observed on standard searches), then white-naped honeyeaters, *Melithreptus lunatus* (14 g; 16 percent), crimson rosellas, *Platycercus elegans* (131 g; 6 percent), eastern rosellas, *P. eximius* (111 g; 3 percent), and spotted pardalotes, *Pardalotus punctatus* (9 g; 3 percent). The small birds fed almost continuously in daylight, each consuming psyllids at mean rates of about 25 per minute. Rosellas are mainly frugivorous but here

were opportunistically consuming psyllids at mean rates of 48 per minute by plucking leaves and drawing them through their bills by foot. Other birds that became common after bell miners were removed included brown thornbills, *Acanthiza pusilla* (6.3 g; 16 percent of birds observed), which fed on understory insects and some psyllids, and three bark-gleaning species: varied sittella, *Daphoenositta chrysoptera* (13 g; 4 percent), and two treecreepers, *Climacteris leucophaea* (21 g; 2 percent) and *C. erythrops* (25 g; 1 percent). Consumption of psyllids or lerps was estimated by multiplying feeding rates and numbers of each bird species counted. Hence the combined impact of all birds in the 2 months after removal was estimated at 650 psyllids or lerps per minute, compared with 280 per minute before removal when bell miners were dominant.

The greater effectiveness of other birds in reducing psyllid numbers may be due to more than this difference in feeding rate. Bell miners do not always eat the psyllid nymph as well as the lerp (*4*), and exposed nymphs can replace their lerps in 1 or 2 days. Tests on captured birds (*6*) and observations on wild birds (*7*) show that bell miners take a lower proportion of nymphs than do other birds. Bell miners often use their tongues to remove lerps without dislodging the nymphs, although nymphs are equally high in calorific content (*6*). In contrast, birds such as pardalotes sometimes peck twice to remove the lerp and the nymph, or take both in a single peck. Whether natural variations in feeding rates and proportions of nymphs taken by bell miners are related to variations in the food supply has not yet been determined. Lerps can be up to 30 times heavier than nymphs (dry weight) (*4*), though often they are closer in weight. Bell miners may be meeting their energy requirements by selecting lerps and larger nymphs, leaving smaller nymphs to grow and replenish the food supply.

Most studies of birds and insects have shown that birds can control insects most effectively when insect populations are low or localized. The birds' major role is in retardation or prevention of insect outbreaks (*8*), though some instances have been reported where local outbreaks were controlled by invading birds (*9, 10*). In our study the exclusion of other birds by bell miners allowed us to show experimentally that other birds could quickly control a major local insect infestation. The birds that controlled the psyllids are common species in eucalypt forests in Victoria (*11*) and often occur in small nomadic flocks. It appears that in the absence of bell miners, these flocks are capable of cleaning up pockets of infestation as they occur and keeping psyllid populations low by continual predation.

Bell miners prevent this degree of control by their interspecific territorial behavior. Colonies are known to remain in one place from 2 years to more than 40 years (*12*), until the high level of psyllid infestation causes trees to deteriorate or die, or until other events force the birds to move. There are many examples of territorial and nomadic birds in the world's forests, but it is usually hard to show that territorial behavior is effective in defending food supplies. The bell miners have developed their territoriality to an extent where its effects have a visible impact on the habitat. Our experiment shows that their interspecific territoriality results in an abundant and exclusive supply of psyllids and lerps for bell miners.

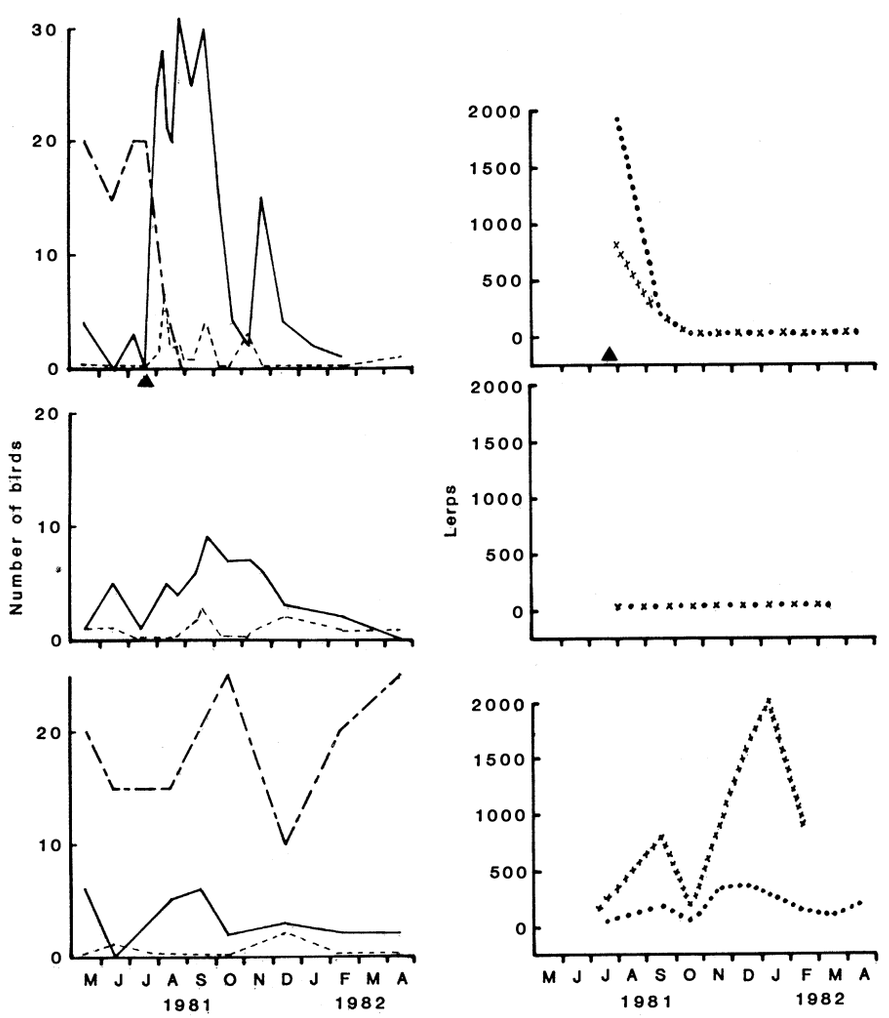

Fig. 1. Birds (left) and lerps (right) counted at the experimental site (top), healthy control (middle), and psyllid-infested control (bottom). Symbols: – – –, bell miners; ——, other birds that eat psyllids and lerps; ------, birds that glean mainly from bark; xxx, lerps per tray; ●●●, lerps per 100 leaves; ▲, when bell miners were removed from the experimental site.

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Is Cytosolic Ionized Calcium Regulating Neutrophil Activation?

Abstract. *The concentration of cytosolic ionized calcium, $[Ca^{2+}]_i$, was measured in intact neutrophils by use of a fluorescent indicator trapped in the cytoplasm. A given rise of $[Ca^{2+}]_i$ elicited by the chemotactic peptide formylmethionylleucylphenylalanine (FMLP) was associated with a much greater degree of superoxide generation and myeloperoxidase secretion than was the same or larger $[Ca^{2+}]_i$ produced by a specific calcium ionophore, ionomycin, which bypasses cell surface receptors. Thus, FMLP appears to generate some important excitatory signal in addition to a rise in $[Ca^{2+}]_i$, and exocytosis and superoxide generation in neutrophils may not be simply dependent on $[Ca^{2+}]_i$ as is widely supposed.*

The production of oxygen radicals and secretion of lysosomal enzymes by neutrophil leukocytes are vital links in animal defenses against infections. These neutrophil responses are conveniently elicited in vitro by various compounds that bind to specific cell surface receptors. It is generally thought that neutrophil activation occurs by raising the concentration of cytoplasmic free Ca^{2+}, $[Ca^{2+}]_i$, which then triggers superoxide generation (*1*), enzyme secretion (*2*), actin gel-sol transitions (*3*), and locomotion (*4*).

However, the difficulty of measuring $[Ca^{2+}]_i$ directly in small mammalian cells in suspension has been a major obstacle in studying the role of $[Ca^{2+}]_i$ in the mechanism of transmembrane signaling. New methods for loading either fluorescent Ca^{2+} indicators (*5*) or Ca^{2+}-sensitive photoproteins (*6, 7*) into the cytoplasm of small intact cells have been described. Using erythrocyte-leukocyte hybrids, loaded with the photoprotein obelin, Hallett and Campbell (*6*) detected a rise of $[Ca^{2+}]_i$ when the cells were exposed to a number of stimuli. However, the use of virally fused cell hybrids is a laborious technique that involves a major rearrangement of the plasma membrane, the main target in neutrophil activation. Moreover, the quantitative and causal relationships between $[Ca^{2+}]_i$ and neutrophil responses have not yet been shown.

In neutrophils $[Ca^{2+}]_i$ can now be easily measured with a fluorescent indicator trapped in the cytoplasm of intact cells according to the method described by Tsien *et al.* (*5*). Using this procedure, we investigated the effect on exocytosis and superoxide (O_2^-) generation of increasing $[Ca^{2+}]_i$ either with ionomycin, a specific Ca^{2+} ionophore, or with the chemo-

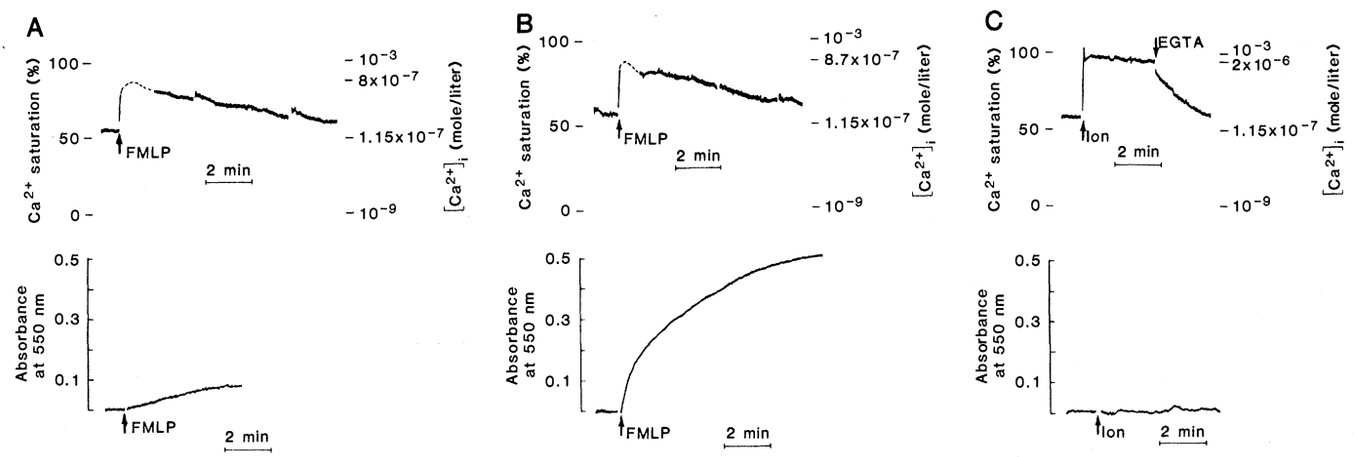

Fig. 1. Effect of FMLP and ionomycin on $[Ca^{2+}]_i$ and O_2^- generation in Ca^{2+} medium [138 m*M* NaCl, 6 m*M* KCl, 1.2 m*M* P_i, 1.2 m*M* $MgSO_4$, 1 m*M* $CaCl_2$, 5.6 m*M* glucose, 5 m*M* $NaHCO_3$, and 20 m*M* Hepes (*p*H 7.4 at 37°C)]. Extracellular calcium concentration, 10^{-3}*M*. (Top) Quin2 fluorescence. (Bottom) Cytochrome c reduction. (A) Quin2 content 0.6 nmole per 10^6 cells. FMLP when added was 0.34 μ*M*. (B) Cells from the same batch of quin2-loaded neutrophils were treated with cytochalasin B (5 μg/ml) for 5 minutes at 37°C. This treatment had no effect on $[Ca^{2+}]_i$ as such. FMLP concentration was the same as in (A). (C) Cells from the same batch of quin2-loaded neutrophils. Ionomycin (*Ion*) when added, was 1 μ*M*; EGTA when added was 4 m*M*. Neither $[Ca^{2+}]_i$ nor O_2^- production in response to ionomycin addition were affected by prior treatment with cytochalasin B. The cell numbers were 5×10^6 and 2.5×10^6 cells per milliliter for quin2 fluorescence and cytochrome c reduction, respectively. The dotted lines represent the graphically redrawn kinetics of $[Ca^{2+}]_i$ rise, since FMLP induces a decrease of cell autofluorescence that is larger and is irreversible in the presence of cytochalasin B. The autofluorescence change is complete in about 60 seconds. The correction was made as follows. At 10-second intervals, the actual fluorescence rise of quin2-loaded cells was corrected for the corresponding decrease of fluorescence in a sample of unloaded cells, at the same excitation and emission wavelengths. The autofluorescence represents 25 percent of the total signal. The autofluorescence decrease is 8 percent of the net fluorescence increase induced by FMLP in quin2-loaded cells in (A) and 35 percent of the net increase in (B). The higher the concentration of quin2 trapped in the cells, the smaller is the correction necessary. No effect on autofluorescence was observed after ionomycin. Interruptions occurred in the traces when the sample compartment was opened and the suspension stirred. The calibration of quin2 fluorescence as a function of $[Ca^{2+}]_i$ was similar to that used for lymphocytes (*5*); that is, quin2 was released from the cells with 0.1 percent Triton-X100 and minimum and maximum fluorescence were recorded at 10^{-9}*M* Ca^{2+} and 10^{-3}*M* Ca^{2+}, respectively. Intermediate values of $[Ca^{2+}]_i$ were calculated by assuming an effective dissociation constant of 115 n*M* for Ca^{2+} binding to quin2, the same as that used for lymphocytes (*5*), on the assumption that intracellular *p*H and $[Mg^{2+}]$ in neutrophils are not significantly different from those of lymphocytes. Excitation and emission wavelengths were 339 and 492 nm, respectively (*5*). The mean resting $[Ca^{2+}]_i$ was 126 ± 14 n*M* ($N = 20$). Some variability in the magnitude of $[Ca^{2+}]_i$ rise, O_2^- production, and MPO release stimulated by FMLP was observed between various batches of cells and from different donors. We do not know whether these differences are due to different proportions of cells responding to FMLP, or to intrinsic differences between batches of cells or donors, or both. The effects of ionomycin were quite constant.