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Widespread ground-nesting in a large population of feral rock pigeons (*Columba livia*) in a predator-free and urban native forest

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Abstract: We found widespread nesting on the ground in a large population of feral rock pigeons (*Columba livia*) in an urban, but predator-free native forest reserve in Christchurch, New Zealand. Ninety-seven percent (n = 77) of rock pigeon nests were located on the ground, with most placed either at the bases of large kahikatea (*Dacrycarpus dacrydioides*) trees or under a tangle of vines on the forest floor. Clutch size was 2 eggs in all nests, with a hatching success of 93.9% in nests that survived to the hatch stage. Overall nest success was higher (60.0%) than in other populations of rock pigeons, with half of nest failures attributed to culling of the population that occurred during the course of our study. On average, rock pigeons fledged 1.60 chicks per successful nest. No ground nests were located outside the boundary of the predator-proof fence, suggesting pigeons were able to assess predation risk when selecting nest site location. Ground nesting by rock pigeons may be a way to avoid damage to nests in the canopy by strong winds or predation from aerial predators such as harrier (*Circus approximans*), which also occur in the reserve. Based on density of nests, we estimated a breeding population of 226 to 258 rock pigeons in the 7.8 ha reserve. The high number of pigeons in the reserve highlights the need for further studies on how populations of introduced species of birds in New Zealand respond to control of mammalian predators and the effect this may have on sympatric native species.

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INTRODUCTION

Island avifaunas around the world have been devastated by introduced mammalian predators (Blackburn *et al.* 2005). In New Zealand, introduced predators have played a major role in the extinction of at least 76 species of birds, comprising 31% of species present at time of human arrival (Holdaway *et al.* 2001). As many surviving species are currently threatened by introduced predators, conservation measures have focused on reducing or eliminating introduced predators, often with spectacular success (Moorhouse *et al.* 2003; Whitehead *et al.* 2008). Early control measures targeted offshore islands, where introduced predators could be more readily removed and reinvasion minimised

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(Towns & Broome 2003). More recently, the use of predator-free sanctuaries has been extended to mainland sites by either ongoing intensive predator control or erecting predator-proof fences around key native habitats and removing all mammalian predators (Innes *et al.* 2019). A number of studies have confirmed positive effects on the populations of most native birds within these fenced 'mainland' islands (e.g. Bombaci *et al.* 2018; Miskelly 2018).

In contrast to the benefits for native species, little research has been done on the effect of predator control on sympatric populations of introduced birds (Morgan *et al.* 2006; Freed & Cann 2009; Baker *et al.* 2014). In some studies, populations of introduced birds increased in response to control of introduced predatory mammals while other species showed no change or even declined (Innes *et al.* 2010; Miskelly 2018; Bombaci *et al.* 2018). A study on the effect of predator control on nest success in passerines in a native forest near Kaikōura confirmed that native species benefited more than introduced species, although nest success was also higher in some introduced species compared to a site without predator control, suggesting that introduced predators could also be limiting population size of some introduced species (Starling-Windhof *et al.* 2011). Given recent proposals to extend predator control over large areas of New Zealand (e.g. Predator-Free New Zealand 2050; Russell *et al.* 2015), there is an urgent need to better understand how introduced birds may respond to predator control and whether there is the potential for increased populations of introduced birds to hinder the recovery of native species.

The rock pigeon (*Columba livia*) was introduced into New Zealand in the 19th century and has since become common and widespread across the country (Higgins & Davies 1996). Rock pigeons were domesticated ~5,000 years ago (Sossinka 1982), and subsequently feral populations have become established around the world, with wild populations continuing to be supplemented from escapes of domestic stock (Higgins & Davies 1996). In New Zealand, the range of rock pigeons increased between two atlas surveys from 1969–1979 and 1999–2004 and the pattern was evident on both the North and South Islands (Robertson *et al.* 2007). Although there are few estimates of population densities of feral rock pigeons in New Zealand, a large increase was noted on the campus of the University of Canterbury, where no rock pigeons were recorded in a 1990 survey, but several hundred were present by 2020 (Stainthorpe 2020).

The nesting biology of feral rock pigeons has not been well studied in New Zealand apart from work by Dilks (1975a,b). In their native European range, 'wild' rock pigeons typically nest on cliffs, or on the walls near the entrance to caves, often in coastal areas (Murton & Clark 1968). In contrast, feral rock pigeons in urban areas typically nest on buildings and under bridges, a pattern that also characterises rock pigeons in their New Zealand range (Higgins & Davies 1996). In both their native European range and introduced New Zealand range, feral rock pigeons typically nest at heights ranging from ~12 m on buildings to as high as 50 m on a power station girder (Higgins & Davies 1996). In this study, we report on a large population of rock pigeons that have become established within a predator-free and fenced urban forest, and which exhibited unusually high levels of ground nesting. We suggest the large population size and change in nesting biology is a response to the low risk of predation in the reserve. We also highlight the implications that widespread predator control may have on introduced bird populations and the need to study its potential effect on native birds.

METHODS

Riccarton Bush (Pūtaringamotu) is a remnant (~7.8 ha) block of native forest located 3.5 km from the centre of Christchurch city (Fig. 1). It is dominated by old-growth kahikatea (*Dacrycarpus dacrydioides*), some of which are more than 600 years old. It is the last surviving representative of lowland forest on the Canterbury plains and thus of important conservation value. In 2004, a predator-proof fence was erected around most of the native forest and all introduced mammalian predators removed, although occasional incursions of rodents (*Rattus* spp., and *Mus musculus*) and brushtail possums (*Trichosurus vulpecula*) occur and are removed by the ranger (M. Steenson *pers. comm.*). The area supports a number of native birds, including fantail (*Rhipidura fuliginosa*), grey warbler (*Gerygone igata*), silvereye (*Zosterops lateralis*), bellbird (*Anthornis melanura*), shining cuckoo (*Chrysoccocyx lucidus*), sacred kingfisher (*Todiramphus sancta*), and New Zealand pigeon (kererū; *Hemiphaga novaeseelandiae*), as well as a variety of introduced birds, including blackbird (*Turdus merula*), song thrush (*T. philomelos*), dunnock (*Prunella modularis*), greenfinch (*Carduelis chloris*), and feral rock pigeon. A 900 m track system through the forest allows visitor access during daylight hours. Adjacent to the native forest is an area of open parkland (~4 ha), consisting of large exotic trees, extensive mown lawns, and a few borders planted with exotic shrubs and flowers (Fig. 1).

We searched for rock pigeon nests within the fenced reserve from mid-September 2020 to late March 2021. From September to January, we searched only for pigeon nests that were directly visible from the public trails, but beginning in late January until late March 2021, we searched a second

Figure 1. Aerial view looking north of Riccarton Bush showing the isolated nature of the reserve and its position in the suburban/urban environment of Christchurch, New Zealand. In this view, the predator-proof fenced area of native forest occupies approximately 2/3 of the reserve on the left (~7.8 ha). The remaining area on the right is occupied by exotic trees, with extensive areas of lawn and flower beds (~4 ha). Photo from Google Earth.

area off the trail that encompassed approximately 25% of the reserve. Searching was carried out by systematically scanning the ground for nests as well as the tree canopy. Visibility varied depending on the thickness of the vegetation, and it is likely some nests hidden in thick vegetation or high in the canopy were missed. A few nests were located by following birds carrying nesting material, spotting accumulations of faeces, or by the sound of begging nestlings. Nests were then visited every 5 to 8 days to monitor their progress. For each nest we recorded its location (nest height), species of nest tree or other vegetation adjacent to the nest, clutch size, and its outcome. Hatching success was measured as the number of nestlings that hatched in nests that survived to the hatching stage and thus is an estimate of egg failure due to infertility or addling. A nest was considered successful if it fledged at least one offspring. Predation was evident either by the disappearance of the eggs from the nest between visits, or the chewed remains of nestlings found in the nest. Nests were considered deserted when no adults were present on two or more sequential visits during the incubation stage (and eggs were cold), or if all nestlings were dead upon a nest visit. To avoid over-estimating nest success, we also calculated nest survival rates using the Mayfield (1961; Johnson 1979) method.

To estimate the population size of rock pigeons in the reserve, we used two methods. The first involved extrapolating from the number of nests we located along the trail system, which was estimated to cover an area of 1.8 ha of the 7.8 ha reserve. This area was estimated by assuming that we could only spot nests within a distance of ~10 m on either side of the trail (i.e., all the nests we located were <10 m from the trail). The second method involved extrapolating the number of nests we located in the area searched off trail (estimated at about 2 ha area of the reserve). To avoid double-counting birds that were re-nesting or sitting on second or third broods, population estimates were based only on the number of nests that were active during November along the trail survey (n = 26), and during February in the off-trail survey (n = 33). It should be noted that both methods are likely to under-estimate population size but we include them here to provide an indication of the minimum number of rock pigeons nesting in the reserve. An additional 18 nests were active outside these two periods and were assumed to be repeated breeding attempts. They were not used in the population estimates to avoid over-estimating population size, but were included in other measures, such as nest location, clutch size, and nest success.

RESULTS

Population size

We monitored 26 rock pigeon nest sites visible from the trail system during November. Assuming we located all nests within 10 m either side of the 900 m long trail (~1.8 ha area), then at least 113 pairs of rock pigeons nested within the fenced area of the reserve ([26 pairs x 7.8 ha]/1.8 ha). This assumes that nests were located randomly with respect to the trails (i.e. birds did not either avoid or nest preferentially close to the trails) and that we located all nests within the search area.

A similar population size was estimated using counts of nests located in our survey area off the trail (but within the fenced reserve). In total we found 33 nests off the trail during February. Assuming we located all nests within the 2-ha area, we estimated 129 pairs of rock pigeons nested in the reserve ([33 pairs x 7.8 ha]/2 ha). As feral rock pigeons form monogamous pairs, this means the reserve supported an estimated breeding population of 226 to 258 birds during our survey period.

Nest site location

A total of 77 nests were found over the course of this study. Seventy-five nests (97.4%) were located on the ground (Table 1; Fig. 2), with most either at the base of a large kahikatea or under a tangle of *Muehlenbeckia* vines. Two nests were located under an elevated boardwalk that lines part of the trail. Only two nests were built above ground level, at heights of 2 m and 2.5 m, respectively (Fig. 3). Three nest sites, all on the ground, were re-used for subsequent broods. These were likely repeat breeding attempts by the same pairs, but birds were not banded to confirm if this was the case.

All nests consisted of a flat platform of small twigs with little evidence that the materials used to build the nest cup differed from the rest of the nest (Fig. 4). At one nest observed during construction, twigs were picked up within a few metres of the nest and the bird then walked to the nest. Two nests were surrounded by many feathers, but these were not concentrated in the central part of the nest as would be expected if used as a nest lining (Fig. 4).

We searched the wooded area outside the fenced reserve (~4 ha) on six occasions between October 2020 and January 2021 but did not find any rock pigeons nesting on the ground, either at the base of the large trees or concealed in the flower beds in the area.

Clutch size and nesting success

We were able to determine clutch size at 63 nests: all nests had a clutch size of two eggs. Hatching success was recorded at 57 nests, and both eggs hatched successfully at 50 nests. At seven nests, only one egg hatched per clutch. Thus, a total of 93.9% (107/114) eggs hatched.

A total of 69 nests were monitored to completion (a few nests were still active when the study was completed), and only 18 nests failed (73.9% nest success): nine nests were depredated and nine nests failed when either the eggs were deserted (five nests) or both chicks found dead in the nest (four nests). For nests in which the number of fledglings could be determined, 31 nests fledged both young, while only one chick fledged in 20 nests. The smaller brood size at fledging was due to either hatching failure (only one egg hatched in 7/20 nests that subsequently fledged one chick) or the disappearance of one nestling before fledging (13/20 nests). On average, rock pigeons fledged 1.60 young from the 51 successful nests. Nest success using the Mayfield method confirmed a low level of nest failure (Daily survival probability: 0.98896; nest success assuming a 46-day nesting cycle [Higgins & Davies 1996]: 60.0%).

Large accumulations of faeces were noted around the edges of all nests (Fig. 2). These became more obvious in nests with chicks but even nests during incubation had a few faeces around the edge of the nest, suggesting adults sometimes did not leave to defecate.

DISCUSSION

We observed a high rate of ground nesting in a large population of feral rock pigeons in an urban, native forest reserve. More than 97% of the nests we located were built on the ground, with most either at the bases of the large kahikatea trees that dominate the forest canopy, or in amongst the tangle of vines that pepper the forest floor. Breeding success was also relatively high, though this was not unexpected as the area is surrounded by a predator-proof fence and all introduced mammals have been removed or controlled when re-invasion is discovered. Based on the area searched, we estimated that between 226 to 258 rock pigeons may be breeding in the reserve, with the majority of them nesting on the ground.

Population size

The large number of feral pigeons we found nesting in Riccarton Bush is a clear indication that reducing or removing introduced mammalian predators can sometimes result in large populations of introduced birds, contrary to the conclusions of some authors that introduced birds are unable to compete with native birds once introduced predators are removed (Bombaci *et al.* 2018; Miskelly 2018).

Figure 2. Examples of rock pigeon nests built on the ground. Top row: distant view of nest showing its position in a vine tangle (A) and close-up with adult incubating (B). Note position of nest to public walking trail. Second row: distant view of nest at base of kahikatea tree (C) and close-up of adult incubating (D). Third row: second example of a ground nest at the base of a kahikatea tree (E) and close-up with two nestlings (F). In each left-hand photo the nest location is indicated by the white arrow. Note the large number of faeces that have accumulated in the nest with nestlings. Fourth row: nest with two eggs built under a fallen log (G) and nest with a well-feathered nestling and one unhatched egg in nest hidden under fern fronds (H).

Figure 3. Examples of rock pigeon nests built above ground level. Top row: distant view of nest showing its position in a vine tangle (A) and close-up with two nestlings (B). Bottom row: distant view of second nest showing its position in the top of a rotten snag (C) and close-up with the adult incubating (D). In both left-hand photos the nest location is indicated by the white arrow.

Figure 4. Variation in composition and structure of rock pigeon nests. Both nests built on the ground. (A) Nest built near base of kahikatea tree. Base and nest platform built of relatively uniform twigs with no obvious difference in material used to line the nest cup. (B) Nest built in vine tangle. Nest built of twigs but those in the nest cup slightly smaller than twigs used in nest base. Large number of feathers were incorporated into the nest but not concentrated inside the nest cup lining.

Table 1. Nest site locations of rock pigeons nesting in Riccarton Bush.

Nest location	**Number of nests**	
	On ground	**Above ground**
Kahikatea (*Dacrycarpus dacrydioides*)	30	0
Muehlenbeckia tangle	32	1
Fallen dead log	7	0
Standing dead log	0	1
Fern clump	2	0
Cabbage tree (*Cordyline australis*)	1	0
Lemonwood (*Pittosporum eugenioides*)	1	0
Under boardwalk	2	0
Total	**75**	**2**

Even more surprising was that the habitat of Riccarton Bush, an old-growth kahikatea forest, seems to be the least likely habitat one would expect to support such a large population of rock pigeons, considering their natural breeding habitat in Europe is largely restricted to sea-cliffs and caves (Higgins & Davies 1996). Although feral birds across their native and introduced ranges now occupy a range of urban and agricultural habitats far from coastal areas, the success with which they have colonised the dense, old-growth native forest in Riccarton Bush indicates both an unexpected high degree of adaptability, as well as raising the prospect that reducing predation risk to save native birds may inadvertently have unexpected consequences on the populations and behaviour of introduced bird species. This is an area that needs further study, especially given plans to extend predator control over large areas of New Zealand (Russell *et al.* 2015).

The effect of the high number of rock pigeons on the native birds and other native flora and fauna was beyond the scope of this study. However, the population of kererū in Riccarton Bush appears small at present, as a maximum of one or two individuals only were seen on a given survey (with none seen on most days). It is not known if kererū numbers might be limited by competition with rock pigeons, though direct competition over food seems unlikely since diets overlap only slightly: rock pigeons mostly feed on grains and seeds while the diet of kererū is largely composed of fruits and leaves (Dilks 1975b; Cramp 1985; Johnston 1992; Higgins & Davies 1996). It is also possible the high density of rock pigeons increases the risk of disease or parasite transmission and this in turn limits kererū numbers. Large accumulations of rock pigeon faeces near nests and around roosts might also increase disease risk for other species, although now the only birds which forage primarily on the ground are introduced species such as blackbirds and song thrushes. Clearly, further work is needed to determine whether the rock pigeons are competing with or hindering population size in native species in Riccarton Bush, and whether other introduced species have similarly increased and affected native bird populations since the removal of introduced predators.

Recognition that the large population of rock pigeons in the reserve may be damaging native species (e.g. large accumulations of faeces smothering native vegetation), led to the managers initiating a culling programme half-way through the course of our study. Pigeons were shot at night while roosting in the trees, and it was estimated that several hundred have been killed since December 2020 (M. Steenson *pers. comm.*). It is almost certain that most of the nine nests we recorded as deserted, either at the egg or nestling stage, were the result of one or both parents being culled as there were no other signs of disturbance as might be expected if desertion was due to a predator visiting the nest. Given the large numbers of pigeons reported shot, it is surprising that failure rates were not higher during our study. We suspect this may because only birds roosting in the trees were targeted for culling, while birds with active nests on the ground were likely sitting on or near their nests at night. It may be necessary to trap birds on the nest if the breeding population in the reserve is to be controlled or reduced.

Ground-nesting behaviour

Nesting on the ground is unusual in rock pigeons. It is likely that pigeons within the fenced area of Riccarton Bush nested on the ground as such sites were safe from terrestrial predators. Indeed, ground-nesting in other columbids, including other populations of rock pigeons, has been linked to a low risk of terrestrial predation but all of these appear to be restricted to isolated islands free of terrestrial predators. For example, Abdulali (1982) reported about 15 ground nests of rock pigeons on the Vengurla Rocks, an isolated islet off the coast of India. Similarly, Nakamura & Kodama (2001) reported that all 24 nests of the Japanese wood pigeon (*Columba j. janthina*) they located on two islets off the coast of Japan were on the ground. Ground-nesting has also been observed in eastern turtle doves (*Streptopelia orientalis*) on small islets in the Ryukyu Islands, an area with few terrestrial predators, and a species that nests arboreally on the mainland (Kuroda 1972).

Ground nesting by rock pigeons has not been previously reported in New Zealand; however, Powlesland *et al.* (2011) found that almost half of Chatham Island pigeon (parea; *Hemiphaga chathamensis*) nests were on the ground or within 1 m of the ground. The authors attributed ground-nesting in parea either as a response to the low stature of the forest, or as adaptations to protection from strong winds (which could blow nests out of trees) and to avoid damage by crash-landing petrels that breed sympatrically. No seabirds breed in Riccarton Bush and the forest canopy is high (>30 m), but it is possible that nesting low or on the ground may be an adaptation to reduce the risk of wind damage, especially from strong north-westerly foehn winds that are common in the Canterbury region. It is also possible that nesting on the ground may minimise predation risk from aerial predators such as swamp harriers (*Circus approximans*), which were observed on several occasions chasing flocks of flying rock pigeons above the forest canopy. Nesting on the ground may reduce the risk of predation, either on the incubating adults or their nests, given that open-country predators such harriers might be less able to locate nests hidden by the dense understorey or on the ground. Whatever the reason, we can rule out the culling of pigeons while roosting as a factor driving birds to avoid nesting in the canopy, as we found ground nesting to be widespread at the start of our study and this was several months before culling first began.

Despite the reserve being fenced and all introduced mammalian predators removed in 2004, we found that half of nest failures were due to predation. The identity of predators could not be determined, but as harriers and kingfishers occur in the reserve, some predation events could have been due to native birds. However, in February a possum was trapped in the reserve and a mouse sighted, suggesting some predation events may have been due to incursions by terrestrial mammals. Nevertheless, our estimates of nesting success (60% by Mayfield method) are higher than those observed in a British study (46%; Murton & Clarke 1968) or a New Zealand study in an area with no predator control (49.3%; Dilks 1975a) as well as in a study of rock pigeons on the University of Canterbury campus (52.3%) undertaken at the same time as our study in Riccarton Bush (Stainthorpe 2020). Nest success was also higher than in rock pigeon populations in their introduced North American range (29%: Schein [1954]; 45%: Preble & Heppner [1981]; 43%: Johnston [1991]).

Rock pigeons were found breeding when the study began in September 2020 and a few pairs were still nesting when we stopped monitoring nests at the end of March 2021, a period spanning at least 6 months. As birds were not banded, it was not possible to estimate the number of breeding attempts per pair per breeding season. In their native European range, five broods may be raised per year (Cramp 1985), and an average of 6.5 broods per year in the United States (Johnston 1992). Given an incubation period of 18 days and nestling period of 28 days (46 days in total), there would be ample opportunity for at least 3 breeding attempts per year in Riccarton Bush. Assuming rates of nesting success (60%) and number of young produced per successful attempt (1.60) do not change seasonally, the breeding population of 113–129 pairs could be producing between 325 to 372 fledglings per breeding season (0.60 x 1.60 x 3 x 113 or 129). If pairs average 5–6 breeding attempts as in other feral populations, then productivity could be double this value. Such a high number would be consistent with the number culled since December if most of the birds killed were young of the year. Although these estimates are approximate only, they do indicate the potential for populations of introduced birds to increase rapidly when released from high rates of predation.

Although most nests we located in Riccarton Bush were on the ground, a small proportion of the population nested above ground in the vegetation. Arboreal nests were more difficult to locate as the canopy could not be seen clearly from the ground in some parts of our survey areas. Nonetheless, it is unlikely we missed large numbers of nests in the canopy as we also searched for accumulations of faeces on the ground as evidence for missed arboreal nests but found most accumulations of faeces were instead associated with large roosting flocks of pigeons. Rock pigeons have been noted to nest in large trees in urban areas previously; for example, Peterson (1986) reported that 24% of rock pigeon nests (n = 54) in Oxford, Ohio were built in trees. The average height of these nests was 9.1 m and none were built on the ground (Peterson 1986). Tree nesting by rock pigeons has also been observed on the University of Canterbury campus, where 10/319 nests were found in trees at heights from 3 to 10 m (mean = 6.8 m; I. Stainthorpe *pers. comm.*). Given that tree nests on campus were positioned on large limbs and readily visible from the ground, we are confident that we did not greatly under-estimate the number of arboreal nests in Riccarton Bush and that most birds nested on the ground.

A precursor to flightlessness in island birds?

Finally, it is tempting to speculate how the rapid change in the nesting biology of rock pigeons, from nesting high on building ledges in urban centres to on the ground in an old growth 'mainland island' forest, might mirror the process that occurs when a species first colonises an oceanic island and encounters novel environmental conditions to which it must quickly adapt. Prior to human arrival, many oceanic islands harboured few terrestrial predators, but instead were home to a diverse array of flightless and terrestrial bird species, including some columbids such as the dodo (*Raphus cucullatus*) on Mauritius, and the solitaire (*Pezophaps solitaria*) on Réunion. Both evolved from volant ancestors and upon discovery by humans, showed a level of naivety to terrestrial predators that quickly led to their extinction. No doubt the pigeons in Riccarton Bush were habituated to a large degree by frequent encounters with visitors, but as we walked around inside the fenced reserve, with the birds relatively unafraid at our approach, one could easily imagine a similar scene that played out in the prehistory of Mauritius, shortly after the ancestors of the dodo had arrived. Finding the ground to be a safe environment both for nesting and feeding, with time, flight became more of a hindrance rather than an asset, and eventually lost altogether.

Of course, rock pigeons are not dodos and evolutionary pathways are not easy to predict. It is not known when rock pigeons first started nesting on the ground in Riccarton Bush, but they were not observed regularly in the reserve until after the Christchurch earthquakes of 2010–2011 (*pers. obs.*). The loss of buildings in the city centre may have forced birds to relocate and nest in trees, including those in Riccarton Bush, though this alone cannot explain the shift to nesting on the ground, and instead it appears related to the change in predation risk. Given the rapidity with which rock pigeons have altered their behaviour in response to colonising an area free of terrestrial predators (but with avian predators still present), it is not too far-fetched to imagine that rock pigeons in a Predator-Free New Zealand might head down the same evolutionary trajectory as that once walked by the dodo and solitaire. Although the success of the rock pigeon in Riccarton Bush raises several concerning questions about how predator control may impact native birds through inadvertent increases in introduced birds, it also provides intriguing insights into how quickly some birds can adapt to and exploit new environments, and perhaps even how new evolutionary trajectories may get started in response to a major switch in behaviour.

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